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**THE REGULATION OF APPROACH AND
PREFERENCE BEHAVIOUR IN YOUNG
PRECOCIAL BIRDS**

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The regulation of approach and preference behaviour
in young precocial birds

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Abstract The dissertation centers around the developmental theory of T.C. Schneirla. The fruitfulness and validity of some central proposals in this theory are evaluated within the general field of imprinting. The results from two studies performed by other investigators which have important implications for the theory are reanalysed. The data are found to be in general agreement with Schneirla's theory as are also the results from the empirical studies reported in the dissertation. In the first empirical study the approach and preference behaviour of young domestic chicks was studied in situations where different frequencies of intermittent light were presented singly or in pair-combinations. The data suggest the existence of an approach system and a withdrawal system working in a counterbalanced fashion. In two reports a series of experiments is presented examining the nature of the relationship between general activity during training and the strength of imprinting to a stationary object. The results suggest that the nature of the relationship changes with variations in quantitative aspects of the training stimulation, supporting the idea that the attainment of a balance between internal state and external stimulation is important if the chick is to prefer the familiar object later in a simultaneous choice test.			
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The dissertation is based on the following four papers, referred to in the text by the respective Roman numerals:

- I Bengtsson, H. (1973). Preference behaviour of domestic chicks toward different frequencies of intermittent light presented singly and in pair-combinations. Psychol. Res. Bull., Lund Univ., XIII:5.
- II Bengtsson, H. (1974). Retinal stimulation underlying the approach responses of naive chicks toward moving objects of different diameters. Psychol. Res. Bull., Lund Univ., XIV:2.
- III Bengtsson, H. (1981). Factors affecting the nature of the relationship between general activity during training and the strength of imprinting. Mimeo. Lund University, Lund.
- IV Bengtsson, H. (1981). Effects of variations in training conditions on the nature of the relationship between general activity during training and the strength of imprinting. Mimeo. Lund University, Lund.

A c k n o w l e d g e m e n t s

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The systematic study of imprinting was initiated by Lorenz (1935). His description and interpretation of the phenomenon attracted the attention of many other researchers, and aside from stimulating research it also had a strong influence on the nature of the questions later asked about imprinting. Lorenz did not give any short definition of imprinting, but I think that my definition below catches the essence of what Lorenz and most subsequent investigators have meant by the term:

Social imprinting is the process whereby an initial tendency among young precocial birds to react filially towards a wide range of stimuli is restricted through experience, so that behaviour patterns which indicate a social bond come under the positive control of a more limited class of stimuli.

We can get an idea of what is meant by "behaviour patterns which indicate a social bond" by looking at the criteria different researchers have used in the laboratory to judge whether a social bond has been formed or not. In his book on imprinting Sluckin (1972) presents a list with five major tests of imprinting:

- a. Distress-at-separation test. Chicks and ducklings tend to emit characteristic calls (peeps) when placed in an unfamiliar surrounding and also after the withdrawal of a moving imprinting stimulus. Peeps are not restricted to these occasions, but they have been used as an index of the behavioural control that is acquired or sustained through the imprinting process.
- b. Recognition-at-reunion test. This criterion is based on differences in the strength of approach and following. A comparison is made between birds previously trained with the stimulus and untrained birds, or between birds trained under different experimental conditions. There are some difficulties associated with the use of this criterion so caution is needed when interpreting the results. Some researchers have also wanted to stress that imprinting is not a process of response acquisition but a process of object acquisition thus requiring a discrimination test.

c. Choice test. This is the standard test of imprinting in which the bird is offered a choice between familiar and unfamiliar stimuli. Choice of the familiar is taken as indicating imprinting, but care must be exercised to ensure that the stimulus is approached not only because of a higher unlearned attractiveness. It has been argued that under certain circumstances the tendency to explore the unfamiliar should be facilitated by the existence of a social bond. However, given the way that imprinting experiments are ordinarily carried out and the results that have been obtained, it seems reasonable to conclude that the choice test is valid.

d. "Run-to-mother" test. In this test the young bird's reaction to some form of disturbance is studied in a testing field which contains the moving imprinting object. Increased proximity-seeking under these circumstances has been used as a criterion of attachment. However, it is worth noting that only if the disturbance consists of the appearance of a strange object is this a clear-cut test of object discrimination.

e. "Work-for-reunion" test. The idea behind this test is, that at a more advanced age, viewing of the imprinting stimulus will function as an incentive and reinforcement only for birds which have developed an attachment to it.

In the definition of imprinting presented above we can trace the implicit assumption of an underlying behavioural control system that organizes these behaviours and justifies the use of attachment or social bond as a theoretical construct. Although much debated when applied to human development (see e.g. Ainsworth, 1972), the value of an attachment construct has generally been taken for granted in imprinting research.

Another implicit assumption in our definition of imprinting is that there is one way leading to the establishment of a social bond. This notion has been seriously questioned by Hess (1973). He distinguishes between association learning processes and imprinting processes which can produce behavioural effects with a "short-term similarity". According to Hess imprinting is a distinct genetically programmed learning mechanism which leads to more complete and permanent effects and also entails a more rapid object acquisition than association learning.

In the experimental study of the development of social bonds two fields of behaviour investigation merge. On the one side we have studies aimed at an exploration of the nature and development of initial preferences, and on the other side we have the imprinting studies proper which deal with factors influencing the restriction of these initial preferences to a more limited range of stimuli with which the animal has had some form of experience. In the present dissertation, studies I and II focus on the first aspect whereas studies III and IV are empirical studies employing an "imprinting paradigm". The dissertation summary is divided in two parts in line with this distinction.

Initial Attractiveness of Visual Stimuli

Early research established that precocial hatchlings are attracted to a wide range of visual stimuli. It was equally clear, however, that not all stimuli were equally effective in evoking approach responses (Sluckin, 1972). Movement and intermittency were found to be two especially potent stimulus parameters. The developmental origin of these early preferences has been explored by means of genetic selection and in studies which have investigated the extent to which external influences during the embryonal and early post-hatch stages bring about modifications in the behavioural end-product. Some of these studies use an experimental paradigm where the developing bird is exposed to a stimulus whose attractiveness to the animal is later assessed in a discrimination test and thus resemble the imprinting studies proper. As in other fields where gene-environment interaction is a major focus of inquiry, investigators differ in the extent to which they believe a specific behaviour to be due to maturational scheduling. Simner has performed a series of experiments from an extreme environmentalistic starting position to explore the origin of the young precocial bird's strong approach reaction to lower rate visual flicker (Simner, 1973; 1974; 1975; 1976; 1978; Simner and Kaplan, 1977). Since flashing light was used as an experimental stimulus in the empirical studies of this dissertation, I shall present the major findings of Simner and his co-workers at some length.

Influenced by the developmental views of Kuo (1932) and Schneirla

(1965), Simner advanced the hypothesis that the attractiveness of intermittent stimulation derives from a long-term prenatal exposure to auditory and/or tactile stimulation from the fetus's own heart beat. Simner's tests of this hypothesis proceeded along three lines:

1. A thorough examination of the parameters of intermittent stimulation to establish the exact stimulative basis for the approach reactions.

2. Experiments to establish when in the course of development the attraction first begins to emerge.

3. An examination of the possibility to modify the chick's preferences by prenatal exposure to intermittent stimulation with other characteristics than the heart beat.

The experiments showed that the chicks' approach was strongest at visual and auditory pulse rates in the vicinity of 4/sec which corresponds well with the chick's prehatch heart beat rate. It was also possible to establish that this differential attractiveness was due to differences in flash rate and not to parameters such as light/dark ratio, peak intensity of each light pulse, light pulse duration or interflash interval.

Findings were first divergent as to when this preference for 4 flashes per sec over slower and faster rates begins to emerge. Later findings however, indicated that this preference cannot be clearly specified in relation to hatch time but is related to the developmental age of the chick and begins to arise between 512 and 530 hr after the onset of incubation. During this period there is a decline in the attractiveness of nonflashing light which accounts for the differential approach behaviour more than an increase in the approach-eliciting capacity of 4 fps.

Individual differences in the chick's attraction toward the optimal rate stimulus were found to be stable and not due to transient states or to differences in locomotor ability among chicks. Those chicks least attracted to the 4/sec rate did not exhibit a stronger approach to an alternative rate.

So far the results presented are consistent with the cardiac self-stimulation hypothesis, but additional findings led Simner to discard

this hypothesis. Efforts to modify the chicks' normally exhibited preference pattern by exposing the embryo to intermittent stimulation proved largely unsuccessful. In particular, an attempt to establish an attraction to a normally nonpreferred intermittent auditory signal by long-term prehatch exposure failed (see also Dimond and Adam, 1972). Furthermore, the most attractive intermittent signal was not found to be identical to the fetus's own heart beat. A square wave white noise signal matched in rate and mean intensity with the pulsative heart beat sound was more attractive as was also a similarly matched white light signal.

These findings led Simner to turn to another biological rhythm as an alternative source of the peak attraction around 4 fps. Not only the chick's prehatch heart beat centers around this rate but also the chick's alpha rhythm during the first several days after hatching. There are different ways in which this fact can be linked in an potentially explanatory way to the chick's preferences (Simner, 1975). The most promising of these, I think, is the hypothesis that the chick's rate preference is a function of the degree of electrophysiological excitation which these rates produce. An optimal synchronization of neuronal activity is produced when intermittent light matches the alpha frequency in rate (Halstead et al., 1942), and Peters et al. (1958) found that the maximum amplitude of the visually evoked response recorded between the optic lobe and cerebellum in newly hatched chick results from stimulation with light pulses around 5 fps. More will be said about this in the next section.

An "intensity" model of early approach and preference behaviour

As we have seen above, Simner had to thoroughly examine what constitutes an optimal intermittent stimulus in order to reach a conclusion regarding the validity of the cardiac self-stimulation hypothesis. Simner's research was influenced by the developmental theory of Schneirla integrating ideas on behaviour ontogenesis and ideas on the stimulative basis for approach (Schneirla, 1959; 1965). According to this theory, which is called the biphasic approach/withdrawal theory, young organisms are attracted to a broad range of stimuli because these stimuli are equivalent in quantitative neural-

input effects. Schneirla argued against the view that innate figural schemata play a role in the regulation of initial postnatal responses, and as an alternative he derived a quantitative basis for the responding. He proposed that stimuli for approach are those producing neural-input effects which are quantitatively low, regular, and limited in their ranges of magnitude, whereas stimuli for withdrawal yield neural-input effects which are quantitatively high, irregular, and of variable, extensive ranges. According to the theory, an organization of proximal sensory functions in the outlined biphasic way during embryonal development is a forerunner to the corresponding functioning of distance modalities (hearing and vision). The organization is reached through a progression in which contributions of maturation are seen as inseparably interrelated with the contributions of energy changes in the environs, among which the role of embryonic self-stimulation is particularly stressed. Thus, during the course of development overt approach reactions accompanied by reinforcing internal processes come increasingly under the control of low-intensity stimuli through contiguity learning. It is also stated that the organization of withdrawal reactions has reached a less advanced stage at birth or hatching, because disruptive processes are infrequently evoked during embryonal development.

Part of the empirical evidence used to build this theory came from studies of early approach responses in birds. More recent studies of chicks' reactions to intermittent stimulation have produced results which are consistent with Schneirla's theory. The probability of obtaining approach reactions increases up to rates of $4\frac{1}{2}$ pulses per sec and then decreases at higher rates. (Gottlieb and Simner, 1969; Kovach, 1970; Fischer, 1972; Simner, 1973). Not all of these studies were designed to study withdrawal reactions, but Fischer (1972) noted that when tones were emitted at a rate of 16/sec chicks crouched more often and seemed quieter than at lower rates. Simner (1973) obtained difference scores between time spent in an approach area and time spent in a withdrawal area and found negative mean difference scores mostly at rates of 12/sec and higher in different age groups. However, withdrawal reactions can also be found at lower rates of auditory and visual stimulation, but at these rates they are typically counterbalanced by approach reactions (Gottlieb and

Simner, 1969). Simner (1978) showed that some chicks approach at most rates whereas others are "withdrawers". For both auditory and visual stimulation an inverted U-shaped relationship has also been found when the intensity of an optimal rate stimulus has been varied, i.e. approach has been strongest at intermediate levels of intensity (Fischer and Gilman, 1969; Kovach, 1970).

So far the review has covered studies which have investigated responses in relation to one localized source of stimulation. Recently, Kovach (1980) working with Japanese quail chicks and a mass-screening procedure, has provided extensive data on preferences when pairs of stimuli are presented. Effects of variations in flash rate, flash amplitude, luminance, and colour were studied in a design which, in most cases, presented the day-old quail chicks with a choice between a flashing and a nonflashing stimulus. The scope of the study and the large number of subjects used (in total 18225 chicks) make Kovach's study a most important contribution to this field of research, and an effort will be made here to analyze the implications of the findings for Schneirla's theory, since these are not clear from the presentation of data. In this section results obtained with acromatic light stimuli will be examined, whereas a discussion of colour will follow in the next section.

The part of Kovach's study which is of present interest consists of three interrelated experiments where the interpretations arrived at in one experiment provided the basis for the next one. Unfortunately, this progression obscures the more parsimonious interpretation of the total amount of data which I shall present below.

Most data were collected by the use of nonflashing light stimuli and two flicker rates, 3 and 9 fps, respectively. Additional rates were used only in one of these three experiments and, for simplicity, I shall leave out the data obtained with these rates and concentrate on the 42 stimulus pairs involving the two flicker rates mentioned above and the nonflashing stimuli. Stimulus specifications and the direction of choices obtained are presented in Table 1.

Table 1. Preference behaviour of Japanese quail chicks toward flashing and nonflashing light stimuli. Statistically significant preferences are indicated by continuous lines and directions of statistically non-significant trends are indicated by broken lines. Data from Kovach (1980). Note that mean luminances are given.

Mean luminances of flashing stimuli (in lux)	Luminances of nonflashing stimuli (in lux)	Choice-directions at two different flash rates (flashing vs non- flashing stimulus)		Pair number	
		3 fps	9 fps		
1.07	2.15	←	←	1	19
10.75	21.5	←	←	2	20
33.9	67.8	←	←	3	21
45.2	90.4	←	←	4	22
59.2	118.4	→	→	5	23
80.7	161.4	→	→	6	24
107.5	215.0	→	→	7	25
1.05	30.45	←	←	8	26
6.30	25.2	←	←	9	27
15.75	15.75	←	←	10	28
18.9	12.6	←	←	11	29
29.4	2.1	←	←	12	30
10.75	304.5	→	→	13	31
63.0	252.0	→	→	14	32
157.5	157.5	→	→	15	33
189.0	126.0	→	→	16	34
294.0	21.5	→	→	17	35
10.75	588.0	←	→	18	36
Both stimuli flashing					
Mean luminance of brighter stimulus (in lux)	Mean luminance of dimmer stimulus (in lux)	Choice-directions at two different flash rates (brighter vs dimmer stimulus)		Pair number	
		3 fps	9 fps		
294.0	10.75	→	←	37	38
Neither stimulus flashing					
Luminances of brighter stimuli (in lux)	Luminances of dimmer stimuli (in lux)	Choice-directions (brighter vs dimmer stimulus)		Pair number	
30.45	2.1	←		39	
58.8	2.1	←		40	
304.5	21.5	→		41	
588.0	21.5	←		42	

According to Kovach's interpretation of his data the element in a given stimulus compound which primarily governs the choice is either luminance or intermittency. However, there is a seemingly complex interaction between the two stimulus elements so that the preference hierarchy of flash rates changes as a function of increasing luminance and the preference hierarchy of luminance changes as a function of increasing rates of intermittency. Viewed in this way the results are sometimes rather puzzling. For example, given high overall luminance, stimulus choices at 9 fps appear to have been determined by brightness rather than by intermittency whereas intermittency was dominant at 3 fps and at both flicker rates when the overall luminance was lower (pair numbers 8-17 and 26-35 in Table 1). Equally puzzling is the finding that when overall luminance was high and differences in brightness large, the brighter stimulus was avoided at 3 fps and approached at 9 fps irrespective of whether it was flashing or not (pair numbers 17-18 and 35-38).

In Figure 1 I have suggested a model which represents an attempt to account for the interaction between luminance and intermittency. The preference values of the flashing and nonflashing stimuli are here depicted as three functions of luminance with the respective peaks at different luminance values. By comparing the two preference values in a stimulus pair it is possible to derive the direction of choices in 41 of the 42 pair-combinations in Table 1. The one that does not fit the model (pair number 41) is not clearly reported in Kovach's article. If what he says in the text is correct, then the results in all 42 combinations are in agreement with this model.

How does this model relate to Schneirla's biphasic approach/withdrawal theory? If we assume that choices are determined by neural-input effects arranged along a single dimension we have to contend that light flashing at a rate of 3/sec produces a stronger neural-input effect than the rate of 9 fps and the nonflashing stimulus at a given level of luminance, since the peak attraction is reached at a lower luminance value for this rate. That this is a reasonable assumption should be clear from what I said in the last section about

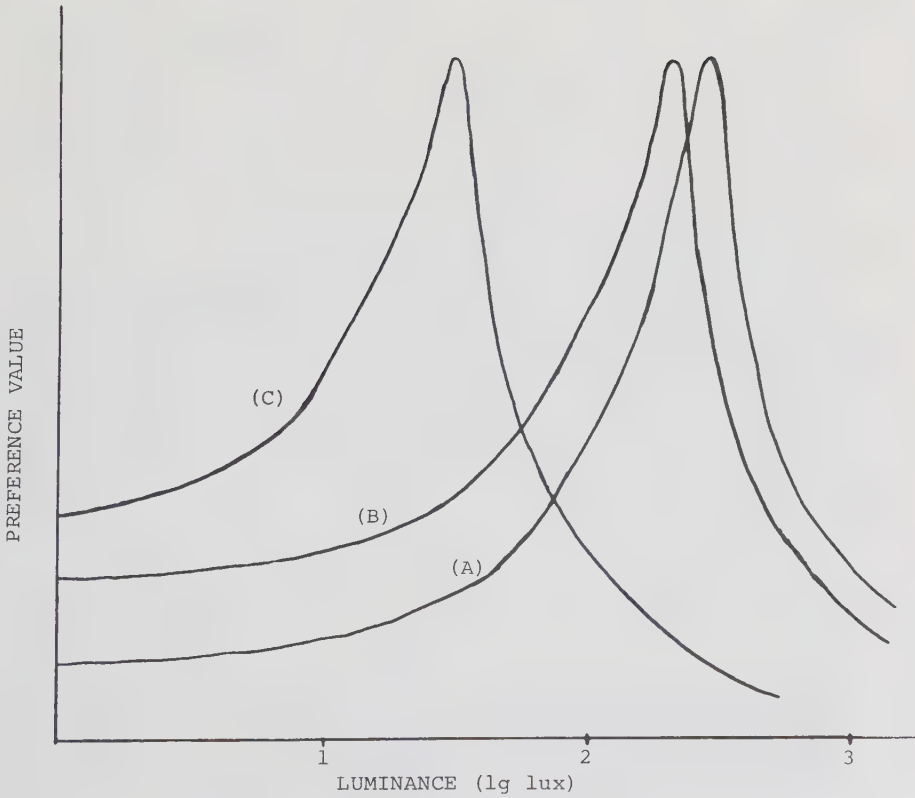


Figure 1. The hypothetical relationship between preference value and luminance at three different acromatic light stimuli. A = nonflashing light; B = light flashing at 3/sec; C = light flashing at 9/sec.

the excitability of the nervous system when the stimulus is in the vicinity of the brain's alpha rhythm. Thus, we find that Kovach's results are quite consistent with Schneirla's position if only we accept that a lower flash rate can produce a stronger neural-input effect than a higher flash rate, which at first might appear somewhat perplexing.

The two major conclusions Kovach drew in this part of his study need to be qualified to some extent in light of the present analysis:

1. There are no fixed preference hierarchies within and between variables of flicker and luminance. This conclusion is clearly substantiated by the data. However, if my analysis is valid this conclusion should not be taken to mean that stimulus choices were not determined by a rigid perceptual hierarchy since the model is consistent with the idea that preference values are derived from a single continuum of neural-input effects.
2. The idea that flash rate preferences are relatable to stable rhythms of self-stimulation during prenatal development or to stable endogenous rhythms of biological activity is contradicted. This conclusion should be qualified since even if the preference value is not exclusively determined by the extent to which the stimulus matches a biological rhythm, it is quite likely that the alpha rhythm is the basis for the stronger effect exerted by the lower rate flashes.

To summarize, data on young precocial birds' reactions to intermittent stimulation appear to be in agreement with the idea that a biphasic organization underlies early approach and preference behaviour. The picture is complicated by the fact that intermittent stimulation includes two important quantitative input-dimensions:

- a. Amplitude of neural input - which is strongest when the pulses are in the vicinity of the alpha rhythm.
- b. Pulse rate of neural input - which is determined by the rate of intermittent stimulation.

That one and the same stimulus can comprise aspects which are widely divergent in their quantitative input-effects was not recognized by Schneirla (1965), whose presentation in this respect was over-simplified.

Colour preferences

Colour preferences in chicks and ducklings have been extensively studied both in reference to pecking and locomotory responses. The findings are to some extent inconsistent which could be due to, for example, strain differences, procedural differences or variations in age and prior experience of the tested birds. Most studies, however, have found red to be the most effective colour for approach in domestic chicks, whereas approach is strongest in response to green in Japanese quail chicks. Some investigators have systematically controlled for intensity differences among coloured stimuli, and the results strongly suggest that the prominent parameter in the colour choice of birds is wavelength and not intensity differences, i.e. fairly large variations in intensity do not affect the preference order of colours. However, in some way chromatic and luminance cues do interact in the processing of information and, as we could see in the last section an interpretation in terms of dominance of one parameter over another can be misleading as stimulus choices may in fact be determined by a single quantitative variable. Since the data analysed in the previous section were obtained in the majority of cases from pair-combinations involving both a qualitative aspect (flashing vs nonflashing stimulus) and a quantitative aspect (differences in luminance), it could prove fruitful to extend the model to cover even interactions between luminance and colour. In general, investigators have employed rather low levels of luminance and, hence, in applying the model in Figure 1 we would expect that the colours most often preferred are those to which the birds are most sensitive, i.e. the peak attraction to the most preferred colours lies at lower luminance levels.

Studies in which a wide range of luminances have been used are rare. Kovach and his co-workers have performed a long series of experiments throughout the seventies on the genotype-environment interaction in behaviour. Among these are examinations of colour preferences in quail chicks involving unselected subjects and subjects from two genetic lines selected for red preference and blue preference respectively. Kovach et al. (1976) report an additive interaction between colour and intensity. Quail chicks normally prefer blue to red, and this preference was enhanced when

the blue stimulus was made brighter (1.0 vs .1 ftc) than the red stimulus, and diminished when red was the brighter stimulus. Since the intensities used were low, interactions of this kind are clearly compatible with the model.

The preference order of colours in quail chicks has a striking similarity to the human photopic curve for spectral sensitivity and to the sensitivity curve for the photopigment, iodopsin, extracted from the avian eye with a maximum at yellow-green and a minimum at the red end of the spectrum (Wald, Brown, & Smith, 1955). The preference behaviour of domestic chicks, on the other hand, tends to be the reverse of this pattern. It is interesting to note, however, that Sedlacek (1972) found the strongest lobar reaction to red in newly hatched domestic chicks (see also Sedlacek, 1971).

Suggestive as these findings may be, we clearly need a more direct test of predictions from the model before we can make any conclusions as to its validity. What we already can say on the basis of existing evidence is that for the model to be valid a pronounced differential sensitivity to colours must exist, since the preference order of colours is preserved despite fairly large differences in luminance between stimuli.

Stimuli differing only in quantity

Turning to cases where young precocial birds are presented with a choice between two physical stimuli which differ only in quantity (luminance or rate), there are data which are not readily reconciled with the model as it stands in Figure 1. By their mass screening procedure Kovach and Wilson (1975) studied stimulus choices of Japanese quail chicks between two lights flashing at the same rate (3/sec) but with different physical intensity. The direction of preferences obtained are presented in Table 2. The results show a general tendency for the higher intensity stimulus to be chosen. In line with the previous discussion there are two alternate ways of viewing these results: (a) Stimulus choices can be seen as determined within wide limits by differences in one parameter relatively independently of other parameters. Thus, if we compare the results in Table 2 with the results in those pair-combinations

Table 2. Preference behaviour of Japanese quail chicks toward flashing stimuli (3/sec) of different luminances. Statistically significant preferences are indicated by continuous lines and directions of nonsignificant trends by broken lines. Data from Kovach and Wilson (1975). Note that mean luminances are given.

Mean luminances of flashing stimuli		Choice-directions
1.05	10.75	————→
1.05	107.6	————→
10.75	107.6	-----→
32.25	322.9	————→

in Table 1 where the stimuli differed only in luminance (pair-combinations 37-42) it is clear that in the majority of all these cases, the higher intensity stimulus was preferred. (Note, however, the discrepant result in pair-combination 37, where both stimuli were flashing at 3/sec). Thus, we may conclude that within the intensity-range studied, choices according to luminance are in the direction of a preference for the higher intensity stimulus.

(b) The assumption that stimulus choices are determined in a biphasic way by quantitative neural-input effects arranged along a single continuum leads to some difficulties which I think, however, can be solved. The results presented in Table 2 indicate that the highest preference value lies at a higher physical intensity for a flash rate of 3/sec than that depicted in Figure 1. Yet the comparability of results should be high, since the same technique was used in both studies, and the chicks were of similar ages. When the curves in Figure 1 were derived, it was assumed that there is an optimal level of stimulation and that the closer a stimulus matches this level the more likely it is to be approached. Could it be that stimulus choices are not always regulated in this way? I think it is reasonable to recognize the existence of two different functional strategies which can underlie approach and preference behaviour, and which can be employed in different types of situations. Given that there is an optimal level of stimulation, approach should in some cases be contingent upon a mismatch between the prevailing input and the optimal input level. This corresponds to a homeostatic mechanism where approach is evoked by a too low level of stimulation.

The locomotory approach responses serve to increase the level of input and, hence, should be directed towards the stimulus of highest intensity in a two-choice situation. If only the lower intensity stimulus exerts an influence upon the animal that is strong enough to start this mechanism we could expect a stimulus to be preferred even if it is more intense than the optimal level. I suggest that we see this mechanism operating in the stimulus choices between luminances in Table 2 and also in the results from the first empirical study of the present dissertation (I). In the latter study domestic chicks were exposed to different flicker rates presented singly and in pair-combinations. The chicks' approach and preference behaviour suggest the existence of an approach system and a withdrawal system working in a complementary and counterbalanced fashion. The results also demonstrate that the stimulus which evokes most approach when presented alone is not necessarily preferred in a two-choice situation, thus suggesting that attraction is relative. A similar effect can be traced in the results of Kovach and Wilson (1975). Confronted with two identical flashing stimuli, a lower proportion of chicks completed all 14 stipulated trials when stimulus luminance was high. In spite of this, making one stimulus less intense resulted in a preference for the higher intensity stimulus.

The way of functioning discussed above, where approach was thought to be evoked by too low level of stimulation, clearly belongs in a context where stimulus magnitude varies along one physical dimension, and approach is likely to lead to a successive increase in the magnitude of input, as, for example, when the animal is approaching a source of light. Similarly, chicks typically behave as if they were maximizing stimulation when they approach a moving object and do not stop until in contact with it (see e.g. Schulman, Hale, & Graves, 1970). However, when stimuli differ in kind it seems reasonable that the animal makes use of discriminatory cues, and that approach can be both triggered by and directed towards the stimulus which most closely matches the optimal level of stimulation. Again, more research is needed to clarify these matters.

Current status of the idea that a biphasic organization underlies early approach and preference behaviour

The prominence given here to Schneirla's basic ideas does not reflect a common pattern in reviews on imprinting (see e.g. Bateson, 1966; Sluckin, 1972). On the contrary, authors have mostly criticized or left without comment the idea that the initial attractiveness of stimuli can be derived solely from their quantitative input effects. Some criticism has been constructive, for example, that provided by Hailman (1970) and Kovach (1970). In other cases, the idea has simply been dismissed on the basis of some conflicting empirical evidence. Schneirla (1965) gave a summary of stimulus characteristics which were likely to evoke approach respective withdrawal processes. Findings have not always been in agreement with this list. However, it must be emphasized that the important thing is the magnitude of neural input which is not a function of stimulus characteristics only. Disproval, thus, would seem to require direct physiological specification and measurement.

The problem of falsification is touched upon in study II of the present dissertation, where data (from Schulman, Hale, & Graves, 1970) which provide one of the most serious challenges to the idea of biphasic processes in young chicks were reanalysed. On the basis of empirical findings existing at the time, Schneirla (1965) proposed that a medium to small, rounded object moving at a regular, low to medium rate away from the subject produces neural input effects optimal for the arousal of approach-processes. On the other hand factors such as large size, sharp corners, movement towards the subject, and high rate of movement were considered to be effective evokers of withdrawal reactions. However, divergent results on two points were obtained by Schulman et al. (1970). These authors found that discs moving towards the chick were more effective in eliciting approach/following than retreating discs, and that withdrawal reactions were absent even when a disc as large as 71 cm in diameter was moved towards the chicks. The data from this study were reanalysed by the present writer in study II with the result that a stimulus parameter was isolated which seemed to account for many of the results. This parameter which is directly related to the speed of the object would lead us on the basis of stimulus intensity to predict

withdrawal reactions in response to rapidly approaching objects but not to objects moving towards the animal at a lower speed, even if the object is of a substantial size. It should be pointed out that in doing the analysis it was assumed that the eyes of the chicks were on a level with the lowest point of the moving object. Likely deviations from this assumption in the real situation do not seriously throw doubt on the conclusions drawn in study II.

With the growth of data in many fields of behavioural research it has become increasingly clear that the systems studied are very complex. Early interpretations tend to be too simple. This does not have to mean that they should be dismissed. Instead it can be profitable to elaborate the basic ideas in the light of more recent data. One of the aims of this dissertation is to evaluate the validity and fruitfulness of some central proposals in Schneirla's biphasic approach/withdrawal theory within the field of imprinting, and also to be suggestive of where and why more research is needed before firm conclusions regarding these matters can be reached.

Theoretical Views on Imprinting

Imprinting was initially described by Lorenz as a distinct learning mechanism differing in kind from other learning mechanisms known at the time, and much of the subsequent research has been performed to test Lorenz's claims for a unique process. According to Lorenz (1935), object acquisition in imprinting is a rapid process producing effects which are irreversible and cannot be erased. It is only operative during a short early period in ontogeny, but the resulting social bond affects behavioural patterns such as mating which appear later in the bird's life. Finally, only supra-individual stimuli, i.e. the characteristics of the species are learned according to this early interpretation of bond formation.

Support for this early conception of imprinting was obtained by Hess (1964) through laboratory analysis. His research revealed five distinctions between imprinting and association learning.

- (1) Imprinting is restricted to a short critical period in the development whereas association learning is not.
- (2) The drugs meprobamate and carisprodol affect imprinting and association learning in disparate ways.
- (3) Massed practise and high expension of effort result in strong imprinting whereas spacing of effort is more effective in association learning.
- (4) The application of aversive stimulation during training leads to stronger imprinting whereas in ordinary learning the animal learns to avoid stimuli associated with painful stimulation.
- (5) Imprinting is strongest to the first object encountered whereas the effects of more recent experiences with other objects are weaker.

All these claims for a unique process have been critizised (see e.g. Bateson, 1966), and there is now a considerable amount of evidence available that seriously question their validity. Most researchers do not accept the idea of a unique learning mechanism but regard the hallmarks of imprinting as products of learning in a specific context. In the imprinting situation we find a young organism with very limited experience involved in learning. The motivational state is characterized by a readiness to emit strong filial reactions to selected aspects of the environment and an initially low but successively increasing tendency to react fearfully to unfamiliar moving objects. This means that normally fear reactions are not likely to interfere with the learning process but, on the contrary, will serve later to protect and strengthen the results of previous learning. Thus, in a "contextual interpretation of imprinting" it becomes a major task to disclose all the constraints and prerequisites that are part of the context within which the learning takes place.

As late as in his book on imprinting in 1973, Hess still argues for the existence of a distinct learning mechanism by which innate behaviour patterns are attached to specific objects. The major characteristics being a critical period outside which true imprinting is not possible, extreme rapidity of bond formation, and permanence of effects. The difficulty to settle the issue has to do with problems inherent in a laboratory analysis when a phenomenon is taken out of

the natural context in which it has evolved and to which it represents a functional adaptation. To gain simplicity and control in the laboratory we pay the price of weak and incomplete imprinting effects with ensuing difficulties among researchers to repeat each others results. Hess argues that many investigators have missed the unique mechanism by training hatchlings outside the critical period or that they have studied a weakened form by using suboptimal stimuli. The way researchers design their experiments reflects their basic beliefs about the phenomenon they are studying. Zajonc (1973) criticized investigators for using experimental paradigms derived from an unproven assumption of imprinting as a rapid all-or-none process, whereas Hess (1973) was equally critical of experiments where chicks are trained for several days before any test is made of the effects of the exposure.

There have been pleas for more standardized procedures so that results would be easier to compare, and there has also been some discussion regarding the suitability of different ways of measuring training effects. On the stimulus side, however, there is a tendency to uncritically equate results obtained with stationary objects and environments, flickering stimuli and moving models. There was a period of search for the "essential stimulus" for imprinting which ended with findings that young precocial birds develop a preference for their static environment. However, this finding does not have to mean that the attachments formed are equally strong, or that the processes involved are identical. It is worth noting that in two of the most clear-cut studies presenting results against the notion of irreversibility (Salzen and Meyer, 1968) and against the claim that imprinting is an all-or-none process (Zajonc, 1973), chicks were exposed to stationary objects during training.

There are findings which point to differences in the way young chicks react to intermittent light compared to a moving object, the implications of which have not been further elaborated. Results indicate that mean approach to an optimum rate flashing light is highest in naive 3-day-old chicks, whereas approach and following

reactions to a moving object are most likely during the first day of life and, at least in chicks reared isolated in light, fear responses to a moving object increase up to the third or fourth day after hatching. (e.g. Bateson, 1964; Kovach, 1970). Furthermore, Dimond (1968) and Adam and Dimond (1971) found that prior exposure to light yielded stronger approach to a rotating disc with a black sector but increased avoidance of a coloured moving object.

A secondary importance is typically given to stimulus type in so called perceptual learning interpretations of imprinting (e.g. Salzen, 1970). Here, emphasis is put on the fact that in imprinting the animal must learn the characteristics of the imprinting object and as a result of this learning a neuronal model will be available representing the familiar. Attachment behaviours will then be organized around this object much because of an inherent tendency of the distinctly strange to evoke fear. In this interpretation the length of exposure to an object or an environment becomes an important factor.

While sharing the basic belief that imprinting can be interpreted in terms of familiar behavioural processes, Hoffman and Ratner (1973) in proposing a reinforcement model of imprinting argued against the idea that the forming of a neuronal model of a stimulus by a young organism necessarily reflects the development of a social bond. Pointing to differences in the way that newly hatched pre-social birds react to moving objects compared to the static environment, the authors argue that moving objects (and lower rate intermittent stimulation) elicit filial reactions and are innately reinforcing. The gradual conditioning of these aspects to initially neutral aspects of the stimulus complex is according to this model an essential part of true imprinting. Thus, these authors make a sharp distinction between imprinting stimuli and nonimprinting stimuli, a distinction that is not found in, for example, Salzen's neuronal model of imprinting, even if his writings reflect a certain ambivalence in relation to this matter. Hence, Salzen (1962) touched upon the possibility of two neuronal model forming systems, and later recommended a closer study of the role of contact reinforcement

in imprinting (Salzen, 1970).

The empirical studies of attachment formation in domestic chicks included in the present dissertation (III and IV) were done with the assumption that reinforcement is an important element in the imprinting process. Under natural conditions heat and contact from the live parent may provide reinforcement. However, in line with the discussion on initial attractiveness of stimuli, it seems reasonable that an additional source of reinforcement is to be found in the magnitude of visual stimulus input. The hypothesis that reinforcing processes in imprinting are contingent upon an optimal level of neural input in relation to the sensitivity of the organism (Moltz, 1963; Schneirla, 1965) represents an interesting alternative to the view that they are innately evoked by certain forms of stimulation. In studies III and IV explorations were made to collect data relevant for this hypothesis which, to my knowledge, has never been systematically tested.

The hypothesis would be strengthened if it could be shown that the same stimulus is not always the most effective stimulus in promoting imprinting. According to Schneirla (1965) sensitivity (and, hence, the optimal input level) is likely to change as a function of adaptation, excitement, age, prior experience, or constitutional differences. Thus, a given stimulation during training would, normally, not be optimal for all chicks trained. This is consistent with findings that the later approach and preference behaviour toward the imprinting object varies with, for example, individual differences in responsiveness or arousal during exposure to the imprinting stimulus (e.g. Martin and Schutz, 1974).

A series of experiments were performed to explore the possibility that reinforcing processes resulting from a balance between quantitative stimulus input and the internal state of the chick play a role in imprinting (III and IV). Subjects were 266 domestic chicks hatched in the laboratory. All the experiments focused on individual differences in arousal or responsiveness during training. As stated above these are known to be related to differences in

training effects, and it also seemed probable that they are associated with differences in the level of optimal input (cf. Berlyne, 1969). In the experiments stimulus conditions during training were varied to see if this affected the nature of the relationship between general activity during training and the strength of imprinting.

The method used was dictated by an effort to control the intensity of stimulus input and to create a set-up where the results obtained from groups exposed to different stimulation during training would be easy to compare. It is an important problem in the field of imprinting that procedural differences make the results of different experiments difficult to compare, and firm conclusions are therefore not readily reached. This problem is amplified here by the vagueness of the arousal concept. An attempt was made to ensure that variations in the training conditions should affect the "attention-getting" value of the imprinting object as little as possible so as not to produce large differences in the length of exposure to it between groups.

The results of the experiments in studies III and IV indicate that individual differences in general activity during training are related to the later preference behaviour in a simultaneous choice test in ways that change with the stimulus conditions during training. Systematic changes were found when quantitative aspects of the stimulation were varied. Differences between groups in average or variation on the indices of general activity were small, and can only have had a minimal influence on the main results.¹⁾ Thus, they support the idea that the attainment of an optimal level of stimulation is essential if the imprinting object is to be preferred to a strange object.

When approach to the single imprinting object at reexposure was systematically related to individual differences in general activity during training, the nature of the relationship was always different from the corresponding relationship between general activity and preference for the familiar in a simultaneous choice test. This makes the picture complex. However, this finding is interesting since it

1) However, it should be pointed out that in experiment 2 of study IV the chicks had shorter latencies during training than during pretraining exposure. Total activity also increased but only in Group C.

has been found that aversive stimulation applied during training promotes approach behaviour but not preference for the familiar in a simultaneous choice test (Barrett, 1972; Ratner, 1976). Together these findings strongly suggest that modes of responding in the two types of situation can develop relatively independent of each other (cf. also the discussion earlier on two hypothetical functional strategies underlying approach and preference behaviour).

Finally, training chicks in one experiment at a more advanced age disclosed a sharp reduction in the effectiveness of one of the stimulus conditions employed during training.

The findings are not readily explained by earlier attempts to account for the role of activity or arousal in imprinting. These explanations have focused on, for example, the amount of muscular effort exerted during training (Hess, 1964), and the length of exposure to the imprinting object (Bateson, 1973; Bateson and Jaeckel, 1974). Also, the view that there is one optimal arousal state is questioned by the findings (Cheng et al., 1979).

There is a general agreement among researchers that arousal during training plays a causative role in imprinting. This is supported by the results from studies in which arousal was experimentally manipulated, for example, by the administration of drugs (Hess, 1973; Martin, 1975; Rajecki and Saegert, 1971). It is against this background, that the correlational approach in studies III and IV must be seen. Unfortunately, the data in these studies offer a complicated picture, and the affects are not always clear-cut even if statistically significant. Hopefully, attempts to manipulate the sensitivity of chicks will provide more definitive answers.

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*Preference Behaviour of Domestic Chicks toward
Different Frequencies of Intermittent Light
Presented Singly and in Pair-combinations*

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A b s t r a c t. - Preference behaviour toward different frequencies of intermittent light was investigated in groups of young domestic chicks (N=260). It was shown that the probability of occurrence of an approach response depended upon the light frequency and that preference was governed in a systematic way in a two-choice situation. Two alternative hypotheses concerning the way that intermittent light affects the individual were presented. According to the first hypothesis the frequency endows the single flash with a positive or a negative valence. The second hypothesis derives drive properties of frequencies from their relation to a hypothetical level of optimal stimulation.

The hypothesis has been advanced that those approach responses which many organisms show to an intermittent source of light may be elicited by the same proximal stimulus as the following-response in conventional imprinting experiments, and may thus depend upon essentially the same mechanisms (James, 1959; Moltz, 1963). This hypothesis derives some support from the fact that in both cases young have an optimum period early in life, and show less positive responses after prior social experience (e.g. Jaynes, 1956, 1957; Guiton, 1958, 1959; James, 1960a, 1960b). Furthermore, a stationary object which is paired with intermittent light may gain the capacity later to elicit approach responses alone (James, 1959). Abercrombie and James (1961) suggest three possible areas in which an explanation for the role played by the intermittent light in this situation may be sought: intermittent light may add to the "attention-getting" value of the objects; it may serve as a non-specific arousal stimulus; or it may act as a reinforcer.

The two experiments to be described here were carried out for the purpose of investigating how the approach responses of dark-reared chicks are affected by various frequencies of intermittent light. In experiment I the question of whether the behaviour of naive chicks in a two-choice preference test are governed in a systematic way by different paired frequencies of intermittent

light is examined. In experiment II the capacity of the same frequencies to elicit approach responses when presented singly is studied. A comparison of the results, with emphasis upon the extent to which choice behaviour in the first experiment can be predicted on the basis of the approach potentials obtained for single components in the second experiment, should provide information about those mechanisms that govern behaviour. Experiment II was also designed to yield some information about the effect of repeated exposure to intermittent light.

The design of the experiments was based to a large extent on the following working hypothesis: Visual flicker is essential for eliciting approach responses to spatial patterns in naive chicks. The head-movements of the birds can be expected to produce a flow of information intermittent in character when the gaze is swept over a pattern rich in contour (Hedman & Marklund, 1969). The importance of head-movements has already been pointed out in the more general context of motion-parallax theories of depth perception (Walk & Gibson, 1961). The amount of contour in a square unit has also proved to be a good predictor of the choice behaviour of naive chicks to different spatial patterns (Karmel, 1969). It is therefore assumed that the proximal stimulation arising from a spatial pattern is roughly equivalent to flicker and that an analysis of the way in which various frequencies of intermittent light affect the individual is necessary for achieving a full understanding of the respective choice behaviour.

Experiment I. Two-choice preference test.

Apparatus

An open "light box" made of white opalized plastic was placed on a stand mounted on a table. The box, 36.5 x 28 x 28 cm, was

vertically divided into two equal halves by a 1 mm Al-plate (the median plane) running parallel with the short sides. Beneath the box the reflectors of two identical stroboscopes (Philips PR 9108) were affixed to the stand. The different frequencies of intermittent light obtained from these stroboscopes constituted the independent variable of the experiment. The bulbs of the reflectors had a flash duration of less than 10 microseconds and an effect of 6-W. The reflectors (13,5 cm in diameter) were placed beside each other with respective optical central axes in the median plane of the light box and with opposite halves of the reflectors covered so that for each the flow of light was restricted to only one side of the median plane. In the bottom of the light box and inside the empty halves of the box the rays of light diverged on their way toward the opening of the box. The latter was covered by two identical plates of frosted glass which, besides further homogenizing the light over the whole surface, also formed the choice plane of the experimental animal. The intensity of the light in each half of the light box was regulated through the use of a grey-filter of the type Kodak Wratten Gelatin ND (Table 1) so that both stimulus fields, i.e. the plates of frosted glass, were held at 2,5 Lux throughout the experiment. The selection of grey-filters was guided by the assumption that the amount of light per second emitted by the reflectors is directly proportional to the frequency.

Any disturbing stimulation from the surrounding dark room was excluded by placing a black plastic box, which had the bottom cut out, on the plates of glass. The effect of the sound from the reflectors was limited by their being located in the median plan of the experimental animal (= the median plane of the light box).

Procedure

The subjects were chicks of Cobb's race obtained from a commercial

hatchery. They were kept socially in darkness until time for testing at age one and two days.

Table 1. The frequency combinations, the respective filters and the resulting light transmission in experiment I.

Frequency combinations (Hz)	Kodak-notation Filter N.D.		Percent of light transmitted	
	lower	higher	lower	higher
1 - 5	-	0.7	100.0	20.0
5 - 10	0.7	1.0	20.0	10.0
10 - 15	1.0	1.2	10.0	6.3
15 - 20	1.2	1.3	6.3	5.0
1 - 10	-	1.0	100.0	10.0
5 - 15	0.7	1.2	20.0	6.3
15 - 25	1.2	1.4	6.3	4.0
1 - 15	-	1.2	100.0	6.3

The experimental animal was placed astride the median line (Table 2, section 1). When put down the chick was surrounded by a small white plastic box which excluded uncontrolled pre-stimulation. The experimenter was situated in the median plane of the apparatus. Half of the chicks were placed with their beaks in the direction of the experimenter and the rest in the opposite direction. A choice was made when the bird stood with both feet on one of the stimulus fields. A "back out" or a very fast choice was accepted if before that the animal had been observed to make head movements to both patterns, i.e. if it could be expected that the chick had received information from both stimulus fields. If no choice had been made within 10 minutes, this was noted and the chick was discarded. A bridge (26 x 7 x 0.8 cm) was later brought into use along the median plane in order to make the putting down easier and to get more clear-cut choices (Table 2, section 2). Furthermore there was

an interchange of frequency between the two reflectors such that a reflector had the lower frequency during one half of the series and the higher frequency during the other half. The latter made possible the testing of possible systematic sources of error in the environment. For two frequency combinations a simplified procedure was tried of not using the white plastic box when putting the animal down (Table 2, section 3).

Results

Table 2. Distribution of individual choices and the number of individuals making no choice.

frequency combinations Hz	Section 1		Choice of frequency		Section 3		Total		No choice $p < \chi^2$
	lower	higher	Section 2 lower	higher	lower	higher	lower	higher	
- 5	1	3	3	8			4	11	.10
- 10	1	3	3	11			4	14	.02
- 15	2	4	5	7			7	11	-
- 20					7	5	7	5	-
- 10	3	3	3	3			6	6	-
- 15	2	2	9	5			11	7	-
- 25					10	2	10	2	.05
- 15	5	1	9	3			14	4	.02

1 square test

There is no indication in the results of an absolute preference for any single frequency or e.g. of the lower frequency in all combinations of stimuli. Still, interesting relationships are found. In the series of combinations with a difference in rate of five Hz the higher frequency is generally preferred. However, there is a successive decrease in this effect with rising frequency. The combination of 1 and 15 Hz, the one with the

largest difference in light frequency, shows the inverse tendency, with a preference of the lower frequency. At a high frequency level a smaller difference seems to be sufficient for the lower frequency to be chosen (cf. 15 - 25 Hz). The preference for the frequency 15 Hz in the combination of 15 and 25 Hz makes fusion improbable at 15 Hz.

A position effect in terms of greater choice of the one reflector than of the other ($P < 0.10$, Chi square test) was found for the combination of 15 and 20 Hz. The latter might be an effect of the inexact way of putting down the chicks in Section 3. No other significant effects of position were found.

Experiment II. Single frequency test.

Apparatus

Five identical runways (92 x 8.5 cm) of black hardboard were placed adjacent to each other on a large plate of frosted glass. Starting plates made of black cardboard were placed at one of the short sides of the runways so that the bottom of each was covered for 25 cm of its length. Black doors located at the line of transition between the starting plates and the glass parallel with the short side could be pushed vertically up and down in all runways at the same time.

Intermittent light was obtained by rotating circular sheets of cardboard provided with a 2.5 cm deep teeth at the circumference in front of the lens of a 250-W projector so that most of its beam was transformed to intermittent light. The speed of rotation was 1 rps and the pulse-to-cycle ratio was 1/2. At fusion the illumination in the runways was approximately 2.5 Lux. Fusion meant that the device for producing intermittent light was replaced by a greyfilter that absorbed 50% of the light so that the amount of light per second was equivalent to that obtained when the light was intermittent.

The stimulus source was situated at a height of 0.5 m, 2.5 m in front of the plate of frosted glass which rested in a stand 1.0 m over the floor. The rays of light from the stimulus source were projected against a glossy white board located below the plate of frosted glass and tilted 45° so that light was reflected in the direction of the latter. The position and the angle were regulated so as to obtain intermittent light over the whole glass. The testing took place in a dark room. In order to further limit irrelevant stimulation a black plastic cover was placed 1 m above the runways.

Procedure

The race and handling of the 100 animals employed were the same as in experiment I. The age at testing was approximately 2 days.

Groups of five chicks each were exposed individually during a 10-minute period to one of five different stimuli. Among the later there were four frequencies of intermittent light also used in experiment I. After a 10-minute pause a second period of stimulation of equal length followed according to the design given in Table 3.

Table 3. Frequencies of intermittent light employed during the first and the second periods of exposure respectively for the different groups in experiment II.

Period of exposure	Groups a - e'									
	a	a'	b	b'	c	c'	d	d'	e	e'
First period	1	1	5	5	10	10	20	20	fusion	fusion
Second period	1	10	5	20	10	fusion	20	1	fusion	5

The testing was made on two different occasions, each of which employed a sample of 50 individuals. All ten groups were re-

plicated on the second occasion. The between-group order of testing was planned so as to neutralize any possible effect due to the time of day at which testing took place.

Each individual was placed on the starting plate and the source of stimulation was switched on. Then for 10 minutes the doors between the starting plates and the plate of frosted glass were removed. The doors were put back after the stimulus source had been switched off. Those individuals who were out on the glass were lifted back to the starting plates. The rest of the individuals were also lifted in order to match the treatment. Furthermore, there was a cleaning of all runways during every pause. A note was made of the time when the individual first made contact with the frosted glass with both feet in each period (a positive choice). In addition a record was made of the individual's position at one minute intervals. If the individual was on the frosted glass, a score of one point was given; otherwise the score was 0. Accordingly, an individual could receive a maximum of 10 position points during one period of exposure.

Results

A Chi-square test of the number of individuals having a positive choice during the first period of exposure (Fig. 1) disclosed a significant overall difference between the groups ($P < 0.01$), groups receiving 1 or 5 Hz being more apt to approach the stimulus. The choice distribution for those groups (a-e) that were not given a changed frequency, yields essentially the same picture at the second period of exposure (Fig. 2). The total number of points scored showed a highly significant increase ($P < 0.001$, Sign test) from the first to the second period of exposure, irrespectively of whether the frequency was changed or not.

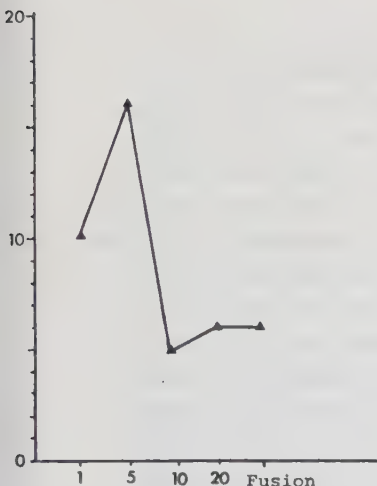


Fig. 1. The number of positive choices as a function of the frequency of intermittent light presented during the first period of exposure.

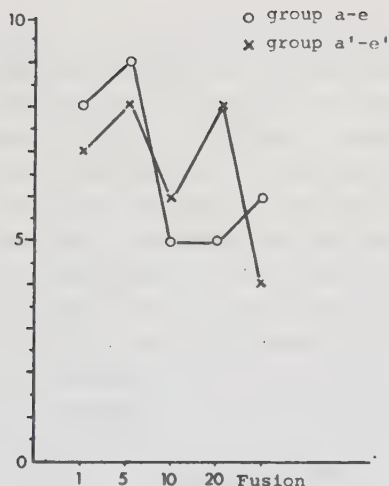


Fig. 2. The number of positive choices as a function of the frequency of intermittent light presented during the second period of exposure.

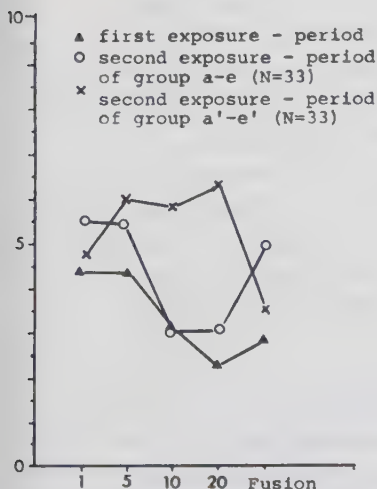


Fig. 3. Mean score as a function of the frequency of intermittent light presented (cf. text).

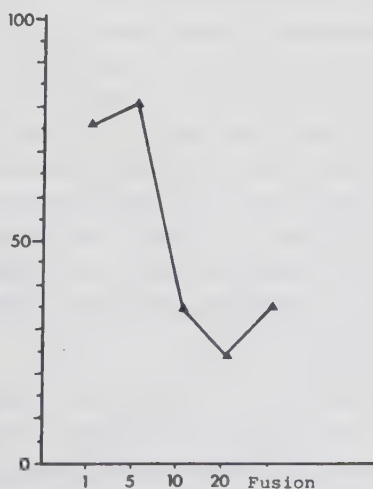


Fig. 4. Percentage of positive choices during the second period of exposure among those individuals not making a positive choice during the first period of exposure.

The apparently deviant distribution for those groups (a'-e') that received a changed frequency may be explained by two factors: (a) 82% of those individuals who made a positive choice during the first exposure made a positive choice also during the second. This finding indicates that scores at 10 and 20 Hz will be high, as these groups earlier received frequencies that were effective in eliciting approach. (b) Those individuals who did not make a positive choice during the first period of exposure but did during the second had a choice distribution (Fig. 4; $P < 0.02$, Chi square test; over-all difference between the groups) that is in agreement with the one shown by the totally naive chicks. This finding indicates that scores at 1 and 5 Hz will also be high. The two distributions in Figure 2 do not give a significant over-all difference between the groups (Chi square test) but the observed trend is supported by the results in Figure 3. The latter shows the number of position points, i.e. how much time the individuals spent on the stimulus plane at each frequency. High values for frequencies of 1 and 5 Hz are confirmed here but the distribution of mean scores (= all position points scored at a certain frequency/the number of individuals making a positive choice to the frequency) may be biased. The test apparatus where five individuals were simultaneously exposed to the same frequency carried the possibility that the number of individuals making a positive choice could have a direct influence upon the tendency to remain on the glass through auditory interaction, which would make the mean score only indirectly dependent upon the frequency of intermittent light.

D i s c u s s i o n

The basic intention of the experiments was to compare approach tendencies in a two-choice preference situation and in a situation involving single presentation of the same frequency stimuli so as to generate hypotheses about the mechanisms under-

lying both. Hence, it is of great importance to ascertain that the experimental variable, the frequency of the intermittent light, actually was the one that mattered in both experiments. The matching that was made to equalize the amount of light per second at all frequencies, was carried out for technical reasons in experiment I by grey filters, which meant that the single flashes at lower frequencies were more distinct, while in experiment II the duration of the flash varied with the frequency. Two independent investigations using one- and two-choice situations respectively make it probable that largely the same results would have been obtained whether or not a matching for amount of light had been made (Gottlieb & Simner, 1969; Larsson & Lundberg, 1970).

The results from the investigation by Gottlieb and Simner (op. cit.) are employed here together with the results from experiment II in order to build a model which forms the starting point for a deduction of the preferences shown in the two-choice situation. The most important complement to experiment II is offered by the opportunity to also study withdrawal responses using the Gottlieb and Simner data. Figure 5 presents the relevant part of the Gottlieb and Simner results. A model to fit these data, empirically based as regards the principal form of the mathematic function involved but hypothetical as regards the details (e.g. size of differences between the eliciting potential of different frequencies), is depicted in Figure 6. The predominant responses of approach at the low frequencies become reversed between 5 and 10 Hz so that the majority of responses at high frequencies are of withdrawal.

From this model the results of the two-choice situation can be deduced in two different ways. The most important require-

ment placed on the model is that it predict the predominant choice of the frequency 10 Hz in the combination of 5 and 10 Hz. A first glance at the results of the one-choice experiment suggests that the opposite preference direction should be expected since the lower frequency has a considerably higher approach potential.

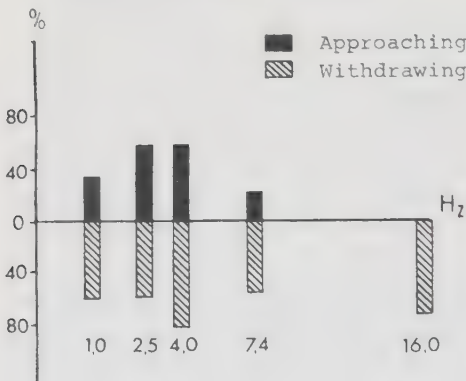


Fig. 5. Percentage of chicks approaching and/or withdrawing at age 40 hours, as a function of the frequency of intermittent light (rearranged from Gottlieb & Simner, 1968).

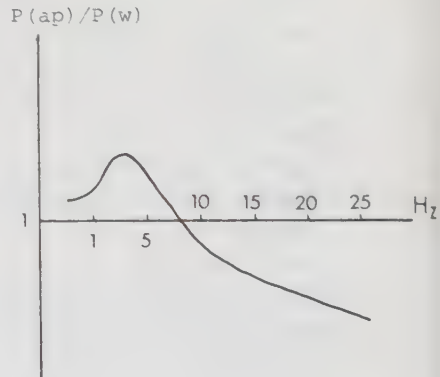


Fig. 6. The probability of approach/the probability of withdrawal as a function of the frequency of intermittent light presented.

According to the first alternative way of deducing the results from the model, $P(ap)$ and $P(w)$ are interpreted as the probabilities that the flash of light will exert attraction and repulsion respectively. Accordingly, the bird orients itself either to the source containing the largest number of flashes or away from it. This implies a two step decision where the decision in the second step is a logical consequence of the first. For example in the combination of 5 and 10 Hz the probability that the total stimulation will induce attraction is greater

than the probability of an opposite result because

$$\frac{P5(ap)}{P5(w)} \times \frac{P10(ap)}{P10(w)} > 1$$

On the basis of such an interpretation it becomes quite a natural prediction that an object paired with intermittent light within a certain range of frequencies will later by itself have the ability to elicit approach responses. An interesting comparison can be made here with the theory of imprinting presented by Schneirla. According to Schneirla, imprinting is established to a low-intensity stimulus primarily because of its capacity to arouse processes of reinforcement which strengthen all approach and following responses to the stimulus (Schneirla, 1965). Bateson and Reese (1968) found that day-old, naive chicks and Mallard ducklings rapidly learned a simple motor response that switched on a flashing light. The same frequency (3 Hz) was highly effective in eliciting approach responses in naive birds tested in another situation.

According to the second alternative way of deducing the results from the model, $P(ap)$ and $P(w)$ are interpreted as indicators of motivational states assumed to arise when a given frequency deviates from a hypothetical "Soll-Wert" where $P(ap) = P(w)$. Low frequencies would give the impulse to increase the stimulus input and high frequencies the opposite. A similar hypothesis is held by Moltz (1963) in his discussion of the responses shown by an organism in the imprinting situation. According to Moltz these responses serve the purpose of adjusting given stimulus magnitudes until an optimal level of excitation prevails.

In comparison with a deduction along the lines of the first alternative the view maintained here has the advantage of be-

ing easier to reconcile with the fact that one observes a preference for one of two frequencies even if both have $P(w) > P(ap)$. The present view is also close to the viewpoint that imprinting implies a satiation of the approach drive (Graves & Siegel, 1968). The latter view derives its prime support from experiments where it has been shown that certain kinds of prior experience like tactile-plus-visual stimulation or social grouping may later inhibit the tendency to approach. The present viewpoint indicates a possible source of such a drive.

To give a correct prediction of choices between higher frequencies, the model as depicted in Figure 5 must be complemented by a factor that accounts for the fact that the relative increase in frequency becomes less for every step on the physical scale. It is probable that this has a counterpart in experience (cf. Fechner's law) which would explain the lack of a significant preference in the combinations of 10 and 15 Hz and 15 and 20 Hz. This complement is required by both alternative interpretations.

An interesting task for future investigation arises through the possibility of unifying the two alternatives into one. The following quotation from Meyer (1968) concerning sensory reinforcement in domestic chicks indicates that both views have something to offer: "..... the light onset as a sensory stimulus acts as a reinforcer but also serves to activate or arouse the organism".

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PSYCHOLOGICAL RESEARCH BULLETIN

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*Retinal Stimulation Underlying the
Approach Responses of Naive Chicks toward
Moving Objects of Different Diameters*

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A b s t r a c t. - In an earlier study, Schulman, Hale and Graves (1970) attempted to identify the visual stimulus conditions which give rise to the initial approach response in precocial neonate chicks. The data from that study are analysed in an effort to identify the critical features of the proximal retinal stimulation that elicit the initial approach response. The analysis shows that the effectiveness in eliciting approach behaviour of an object moving toward the chick is a function of the relative increase in speed of the object's visual angle. This aspect of the stimulation is predictive of the findings on both the relationship between stimulus diameter and stimulus effectiveness and the relationship between stimulus diameter and moment of approach initiation. It is also shown that the absence of withdrawal reactions toward large stimulus objects can be interpreted as supportive rather than nonsupportive of Schneirla's biphasic approach/withdrawal theory.

Schneirla has suggested that the essential features of the stimulation for many responses of young organisms are quantitative rather than qualitative (Schneirla, 1959, 1965). They tend to approach sources of stimulation that excite neural input effects which are quantitatively low, regular, and limited in range of magnitude, and withdraw from those which produce input effects which are high, irregular, and of extensive ranges. According to this view, as the intensity of stimulation is increased from zero it first becomes more effective in eliciting a full approach, but beyond a certain intensity, withdrawal becomes more likely. Qualitative differences in stimulation (i.e., differences in kind) are significant only to the extent that they affect the quantitative input effects. If this suggestion is correct, those situations in which a neonate seems to respond in line with an innate figural schema must be further analysed to reveal the essential quantitative stimulus effects involved. Accordingly, when data arise which seem to be contradictory to Schneirla's biphasic approach/withdrawal theory, the question must always be asked: Has the critical releasing aspect of the stimulation been properly identified?

Schulman et al. (Schulman, Hale & Graves, 1970), examining visual stimulus conditions which elicit the initial approach response in newly-hatched chicks, arrived at the following two results:

(1) initially, chicks were observed to move toward approaching objects rather than to follow retreating ones; and (2) as measured by both response latency and the proportion of birds who responded, stimuli ranging from 10 to 20 cm in diameter were most effective in initiating approach. No withdrawal reactions were found even toward a very large stimulus object. If the size of the stimulus object is the critical feature of the stimulation, i.e., the effective intensity variable, these findings would be hard to reconcile with the biphasic approach/withdrawal theory. Moltz (1963) interpreted the theory to mean that a retinal image decreasing rather than increasing in size constitutes a favourable stimulus for approach/following responses. Also the failure to observe any withdrawal reactions even towards a stimulus diameter of 71 cm casts some doubt on the theory. The absence of withdrawal responses permits an alternative interpretation in terms of stimulus generalization for an optimal stimulus (Schulman, Hale & Graves, 1970). In what follows I will present a more thorough analysis of the proximal retinal stimulation and try to delimit the critical releasing feature of this stimulation as evidenced by the Schulman et al. data. As will be seen, this analysis will permit conclusions to be drawn from the same set of data which, in fact, fully support the biphasic approach/withdrawal theory.

A n a l y s i s o f r e t i n a l s t i m u l a t i o n

A promising lead toward the identification of the critical feature of the stimulation was the finding that an object moving toward the chick is most effective in initiating approach behaviour within a rather limited range of distance from the chick (cf. below). Therefore, the analysis was di-

rected towards the search for an aspect of the stimulation that would be maximally potent within this range of distance.

The visual angle of an object, e.g. a ball, approaching the eye at a constant speed (cm/sec) will not grow at a constant angular speed (degrees/sec). Instead, the angular speed (w) will increase as the ball approaches. The course of the increase will be dependent upon the diameter of the object. The relative increase $\left(\frac{w_2 - w_1}{w_1}\right)$ from one distance interval to the next will reach its maximum value at different distances for different diameters of the stimulus object. Below there are seven diagrams showing, for different diameters, the relative increase in angular speed as a function of the distance of the object from the eye. The calculations are based on the angular increases during intervals of 10 cm when starting 85 cm away from the eye.

Computational example

According to estimations based on tangents, the visual angle of a 20-cm disc will increase 5.78° when approaching from a distance of 45 to 35 cm. The corresponding increase between 35 and 25 cm is 8.92° . Thus the relative increase will be $\frac{8.92 - 5.78}{5.78} \cdot 100\% \approx 54\%$. The estimations derive from the visual angle of the vertical diameter, when the eye is on a level with the lowest point of the diameter.

Relationship to the Schulman et al. data

The diameters in Fig. 1 are the same as were used by Schulman et al. In their study, each chick was given a maximum of five approach-retreat sequences of the stimulus. Of the 108 birds responding, 102 initially approached and only six followed. When the chick started to move, the disc was stopped and the distance at that moment between the chick and the object was noted. The positions of the 95% confidence intervals of the mean response distances are indicated in the dia-

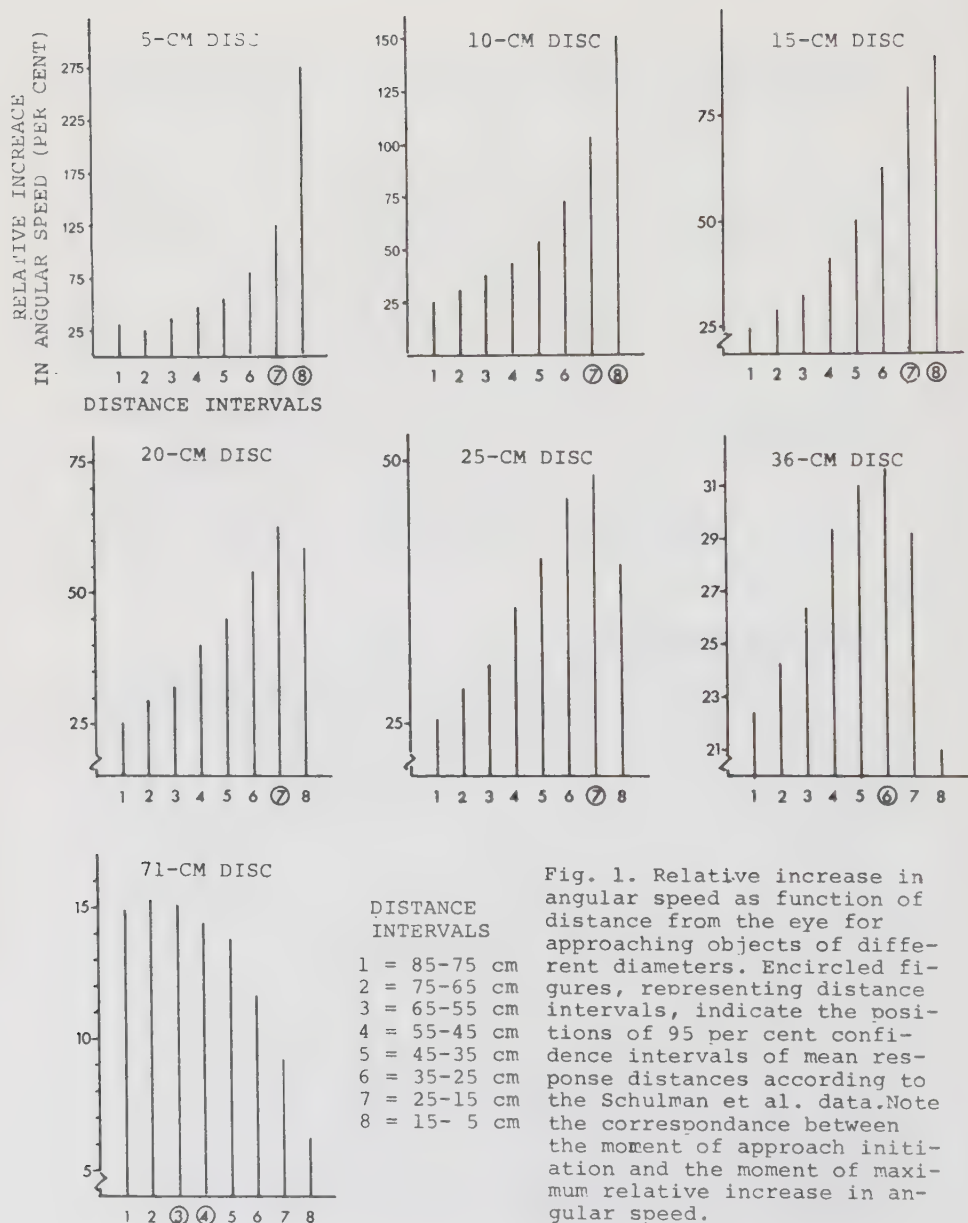


Fig. 1. Relative increase in angular speed as function of distance from the eye for approaching objects of different diameters. Encircled figures, representing distance intervals, indicate the positions of 95 per cent confidence intervals of mean response distances according to the Schulman et al. data. Note the correspondence between the moment of approach initiation and the moment of maximum relative increase in angular speed.

grams (Fig. 1). It is obvious from the diagrams that there is a high correspondence between the moment of approach initiation and the moment of maximum relative increase in angular speed.

Prediction of relative stimulus effectiveness

If this is the critical feature of the stimulation, would it not then be possible to predict the relation between stimulus diameter and stimulus effectiveness? In order to accomplish this the mean relative increase in angular speed of different discs must be expressed in the same unit. This means that one must convert percentage of angular speed into degrees per second. For each disc this is arrived at through multiplication of the mean relative increase in angular speed by the mean angular speed of those intervals used in the denominator in the calculation of the relative increase in each interval.

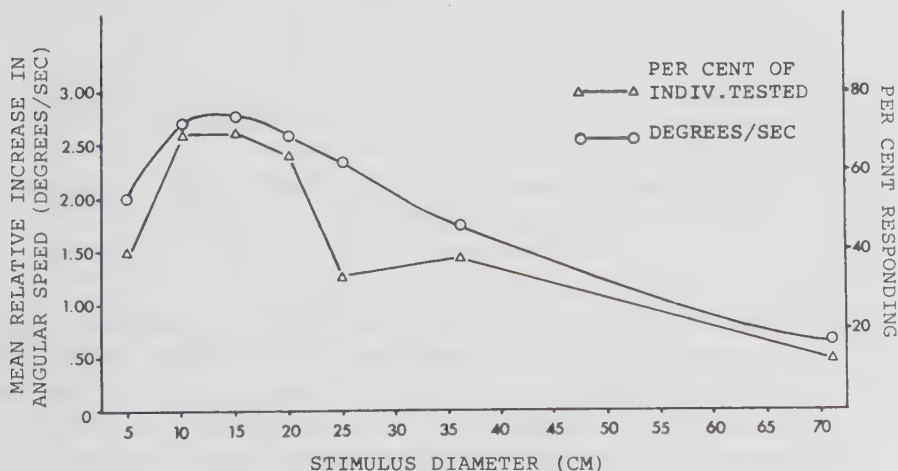


Fig. 2. Predicted stimulus effectiveness and per cent responding as function of stimulus diameter. Per cent responding refers to birds responding during the first approach-retreat sequence according to the Schulman et al. data.

The resulting prediction will be affected by the number of intervals used in the calculation of the means. Insignificant stimulus magnitudes might bias the prediction. Since practically no approach responses were elicited from the chicks at distances greater than 75 cm or less than 5 cm from the eye, the seven 10-cm intervals between 75 and 5 cm were used as the basis for calculating the means. Fig. 2 presents the functional relationship between predicted effectiveness and stimulus diameter. It also shows the different proportions of chicks (N=140) moving toward the object during the first approaching sequence according to the Schulman et.al. data.

Computational example

The predicted effectiveness of the 36-cm disc is arrived at in the following way:

Mean relative increase in angular speed during the seven 10-cm intervals between 75 and 5 cm distance = $\frac{24+26+29+31+32+29+21}{7}\%$ = 27.43%.

Mean angular speed during the seven 10-cm intervals between 85 and 15 cm distance = $\frac{2.69+3.34+4.22+5.46+7.15+9.41+12.16}{7}$ degrees/sec = 6.35 degrees/sec.

Predicted effectiveness = mean relative increase in degrees per second = $\frac{27.43 \cdot 6.35}{100}$ = 1.74.

D i s c u s s i o n

It can be seen in Fig. 2 that there is a high degree of agreement between the prediction based on our analysis and the actual findings. What are the implications of this for the Schneirla theory? Fig. 2 shows that the intensity of what here is assumed to be the critical feature of the stimulation does not uniformly increase with the size of the object. The largest object studied actually produced the least "intense" stimulation. Instead, the intensity is directly proportional to the speed of the object. What this means is that if two stimulus objects of identical size are presented to the animal but one

is moved faster than the other, then the more rapidly moving stimulus produces a more intense neural-input effect. If the speed of the approaching object is made high enough, the biphasic approach/withdrawal theory would predict withdrawal reactions to occur at all diameters. Stimuli approaching the animal and producing a rapidly increasing image on the retina have, in fact, been found to elicit withdrawal and other aversive responses (Schaller & Emlen, 1962; Schiff, 1965; Gupton & Sluckin, 1969). In the study by Schulman et al. the stimulus was moved to the chick at a lower speed than was employed by Schiff and the others cited (10 cm/sec as compared to 25-107 cm/sec on first presentation of the stimulus). Within the low-intensity (low-speed) range, as the intensity of stimulation is increased, it first becomes more effective in eliciting a full approach according to the biphasic approach/withdrawal theory. This prediction is borne out by the Schulman et al. data (Fig 2). It thus appears that these data are supportive rather than nonsupportive of the Schneirla theory.

This analysis highlights the danger of rigidly listing stimuli assumed to be equivalent for neural-input effects to the arousal of approach or withdrawal reactions respectively (Schneirla, 1965). As we have seen, a large object is not always a high-intensity stimulus. Emphasis must be put on the importance of a thorough analysis of the critical features of the stimulation in each specific case.

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FACTORS AFFECTING THE NATURE OF THE RELATIONSHIP BETWEEN
GENERAL ACTIVITY DURING TRAINING AND THE STRENGTH OF
IMPRINTING

by

Hans Bengtsson

Lund, 1981

A b s t r a c t. - Studied attachment formation to a stationary imprinting object using altogether 138 newly hatched domestic chicks. Stimulus conditions during training differed systematically between experimental groups. Measures of the chicks' activity during training, were related to the results in tests of retention. Systematic relationships were found between activity and preference in a simultaneous choice test which required discrimination between the imprinting object and another object. The nature of the relationship was affected by the intrinsic attractiveness of the two objects. Results obtained with an imprinting object of lower intrinsic attractiveness than the unfamiliar object suggested that the former was preferred later in a testing session, if an optimal balance existed during training between the internal state of the bird (as reflected in a measure of activity) and the characteristics of the stimulation.

In his review and critical evaluation of six different interpretations of imprinting, Rajecki (1973) concluded, that in all theoretical frameworks arousal was implicated. Several other studies have also presented evidence for systematic relationships between probable indices of arousal during the initial exposure (training) and the subsequent behaviour of the young bird towards the imprinting stimulus (Fischer, 1967; Bateson, 1973; Bateson and Jaeckel, 1974; Martin and Schutz, 1974; Cheng et al., 1979). In addition, Tolman (1963) demonstrated that changes in wakefulness of chicks over the first 24 hr period after hatching showed a striking similarity to the curve obtained by Hess (1959) for imprinting effectiveness, the so-called critical period. However, the question of why arousal is important cannot as yet be answered with certainty. Two hypotheses, which are not mutually exclusive, emerge from the empirical studies mentioned above:

1. Since arousal most likely affects the amount of attention paid to the imprinting stimulus by the bird, the influence could, at least partly, be an indirect one exerted through the length of exposure. The strength of attachment is dependent upon the amount of visual experience the bird has with the imprinting stimulus during training

(e.g. Connolly, 1968; Zajonc et al., 1973; Bateson, 1974).

2. It could be that the imprinting process requires an optimal level of arousal, i.e., even if the length of exposure could be controlled there would still be differences in the later preference behaviour depending on the chicks' endogenous arousal state during training.

The major support for the latter hypothesis comes from a study by Martin and Schutz (1974). In this study, the birds who completed a stipulated amount of following more rapidly during training were found to exhibit a stronger preference for the imprinting object in a later discrimination test. However, there is an indication that the intrinsic attractiveness of the training object affected the results so that the conclusion above should be restricted to birds trained with an object of high intrinsic attractiveness. The present study explores whether the nature of the relationship between the chicks' activity level during training and measures of retention is affected by changes in stimulus conditions during training. In Experiment 1, chicks were exposed to one of two stationary imprinting objects selected to be of differing intrinsic attractiveness to the chicks. That chicks readily form attachments not only to moving models but also to their static environment has been demonstrated in a number of studies (e.g. Taylor and Taylor, 1964; Salzen and Meyer, 1968; Zajonc et al., 1973).

In the second experiment, the groups were exposed to quantitatively different photic stimulation during the training session with a stationary imprinting object. The length of training was the same for all groups, and it was not possible for the chick to affect the intensity of visual stimulation through approach or withdrawal in relation to the light source.

Experiment 1.

Imprinting objects differ in the extent to which they evoke approach, both during training and after training (e.g. Sluckin, 1972; Martin and Schutz, 1974). This is true not only of moving models but also of stationary objects. Salzen and Meyer (1968) exposed chicks to either a ball or a rectangular sponge which hung in the boxes where

the animals were reared. In subsequent tests of imprinting, the results indicated that the ball was intrinsically more attractive to the chicks. Also when the initial attractiveness was assessed (with no training) the ball was preferred to the sponge.

The aim of Experiment 1 was to study the relationship between the chicks' activity level during training and measures of retention for two imprinting objects of differing intrinsic attractiveness to the chicks. Guided by the findings of Salzen and Meyer, we exposed half the chicks to a rectangular box and the other half to a circular disc.

Method

Subjects. Forty-two Ross chicks were the subjects. Eggs were obtained from a commercial hatchery two days before hatching started. In the laboratory they were hatched in a still-air incubator maintained at approximately 37.5°C. The humidity level was 85-90%. Within 8 hrs after hatching the chicks were transferred to boxes, which were covered with blankets. The chicks were kept in groups of three to eight individuals, the group size depending upon how many eggs had hatched since the incubator was last inspected. The illumination reaching the chicks between delivery of the eggs and training was negligible, since even handling of the chicks was done in almost complete darkness. The light-proof room was maintained at approximately 30°C. Eggs from seven separate batches were used.

Apparatus and procedure. An alley, 60x27x30 cm (length x depth x height), was placed on a large sheet of frosted glass, which rested on a stand 105 cm above the floor. The walls were painted flat black. During the initial imprinting exposure (training phase) a temporary wall was inserted into the alley, so that an area (27 x 18 cm) was formed at one of the ends of the alley according to a random sequence. The imprinting object was located midway along the short side of the alley. For one half of the chicks, the object was a box, 7 x 4 x 12 cm, covered with black velvet. For the other half a disc, 15 cm in diameter, served as the imprinting object. The disc was also covered

with black velvet, and it was fixed to an anglebar which could be pushed in under the wall of the alley. In this way the disc was elevated 2.5 cm above the floor, and a 3.75 cm² metallic square was visible below the disc.

Below the frosted glass floor of the alley, a highly reflective, white board (100 x 60 cm) was mounted in a tilted position in such a way that a beam of light could be projected against it from a source in front of the stand at about the same height as the board itself - thus providing a reflected beam of light which illuminated the alley from below. In this way a situation was created which would limit the possibility of the chicks to affect the intensity of the light to which they were exposed. The source of light was a 150-W slide projector (Pentacon Filius 4) which was placed 2.5 m in front of the tilted board. The amount of light allowed to reach the board was limited to that which had to pass through a small aperture (2 x 2 cm) located close to the slide. The intensity of the light was further lowered by means of a rheostat, and the subsequent illumination of the glass floor (measured by a Lunasix photometer held perpendicularly and close to the glass floor) varied between 4.0 and 4.8 Lux from one part of the training area to the other. The apparatus was situated in a dark room maintained at 23 to 24°C by a radiator with a fan which also provided a homogenous background sound.

The chicks were trained one at a time in the apparatus. The training started at an age of 10 to 24 hr after hatching. The chick was picked up gently and transported to the experimental room where it was assigned to one of the two experimental groups in accordance with a balanced schedule. Special care was taken to ensure that the surroundings were dark whenever a chick was picked up and transported. The chick was placed in a corner at the inserted wall and facing the imprinting object. Exposure lasted for 12 min during which the activity level of the chick was systematically observed. The side of the enclosure had small markings at 9 cm intervals, and the number of zones (9 x 9 cm) entered by the chick during every 30 sec interval were recorded. Two measures were used as indices of the chick's activity level. Start latency was the ordinal number of the

30 sec interval in which 100% of the chick's body was outside the starting zone for the first time. The second measure, total activity, was the sum of all zones entered by the chick with the whole body during the training phase.

When the 12 mins of training had passed, the light was turned off, the chick picked up, and returned to a rearing box after a numbered ring had been fixed around its left leg. In the rearing boxes the birds were kept as before the training phase until approximately 24 hr later (24 ± 4 hr) when the effect of the imprinting exposure was assessed (testing phase). Keeping the chicks together in darkness made it practically impossible to have exactly the same interval for all chicks between the beginning of the training and testing phases. However, it was possible to make observations during the testing phase without knowing the identity of the chick.

In the testing phase the chick was presented with the imprinting object and a novel object. The imprinting object for the one experimental group served as the novel object for the other group and vice versa. The middle part of the alley was used. Two inserted black walls confined a testing field (41.5 x 27 cm) which was divided into three zones (two lateral zones 16 x 27 cm and an intermediate zone 9.5 x 27 cm) by small markings on the side of the alley. The two objects were first presented one at a time and then finally there was a simultaneous choice test. Each of these three sessions lasted for 3 min, and the inter-test intervals were less than 30 sec. The object(s) was/were placed at one of the short sides of the lateral zones, and the starting position of a chick in a testing session was always in the intermediate zone close to the wall opposite to the object(s). The object to be presented in the first session, as well as the lateral zone to be used, was decided by a balanced sequence. The object that was presented in the second session was always placed in the same position as the first object and remained in this position even during the last session when both objects were presented at the same time, one in each of the lateral zones. Before every rearrangement the chick was taken out of the apparatus and was kept covered in the experimenter's fist.

Checks were made at half-minute intervals to determine the position

of the chick. Scores were assigned in the following manner: a) During the first two sessions, +1 was given if the chick was in the zone containing the object, 0 in the intermediate zone, and -1 in the empty lateral zone. b) During the last session, +1 was assigned in the zone containing the imprinting object and -1 in the zone with the novel object. To get a score of +1 or -1 the chick had to be in a lateral zone with the whole of its body. Accordingly, the maximum attraction score in a session was +6.

Results

Table 1 shows the means of the attraction scores obtained during the three testing sessions. The experimental groups differed significantly only in the simultaneous choice test (Mann Whitney test $z = 2.16$, $p < .05$, two-tailed).

Table 1. Means of the attraction scores in Experiment 1 ($n = 21$).

Imprinting object	Testing session		
	Single box	Single disc	Choice test
Box	-.86	+1.29	-.24
Disc	-.38	+1.24	+1.95

Chicks trained with the disc approached this object more than chicks trained with the box.

In both experimental groups the disc was more attractive when presented singly than the box (Mann Whitney test; chicks trained with box $z = 2.47$, $p < .02$; chicks trained with disc $z = 2.86$, $p < .01$, two-tailed). This suggests an unlearned preference for the disc, which is also reflected in the results from the simultaneous choice test where altogether 19 chicks preferred the disc, whereas only 7 chicks preferred the box (Binomial test $z = 2.16$, $p < .05$, two-tailed).

Start latency during training showed no consistent relation to the chicks' responses when the objects were presented singly. However, in both experimental groups there was a significant relationship

between start latency and imprinting as measured in the simultaneous choice test. For chicks exposed to the disc during training there was a negative correlation ($r_s = -.50$, $p < .05$, two-tailed) between start latency and the tendency to be close to the disc, i.e. chicks having short latencies showed the strongest preference for the imprinting object. For the group trained with the box the relationship had the form of an inverted U; chicks preferring the imprinting object having medium latencies. A nonparametric test of relative variation in two independent samples (Ferguson, 1966) was applied to the data and revealed a significant difference between chicks preferring the box and chicks preferring the disc ($U = 3.5$, $n_1 = n_2 = 6$, $p < .02$, two-tailed).

The total activity scores had no systematic relation to any of the attraction scores. In summary, the 12 mins of training had an effect on the chicks' behaviour in the simultaneous choice test between the imprinting object and a novel object, while the object's attractiveness when presented singly seemed not to be affected. Furthermore, the preference behaviour was significantly related to the chick's start latency during training.

Experiment 2.

In Experiment 2 intermittent light was used to create the training conditions which contained quantitatively variable photic stimulation. Chicks' reactions to intermittent light have been extensively studied since James (1959) first called attention to the fact that chicks are attracted to lights flashing at low rates. Generally a peak of maximum approach is reached at a rate of approximately 4 flashes per sec (fps), whereas withdrawal responses occur at higher flashing rates (Gottlieb and Simner, 1969; Kovach, 1970; Bengtsson, 1973; Simner, 1973). In the present experiment four different experimental conditions were created using two rates, 5 fps and 15 fps. The black box used in Experiment 1 served as imprinting object for all subjects, while the disc was used as novel object during the testing phase.

Method

The method in Experiment 2 was the same as that in Experiment 1 except for the differences described above and below.

Subjects. Ninety-six dark-hatched chicks from a total of ten different batches were used.

Apparatus and procedure. The light source used in this experiment consisted of two light bulbs with reflectors (6.3 V; .3 A) placed at a distance of 140 cm from the white tilted board (cf. Experiment 1). The lights could be operated manually and in such a way that the two bulbs were lit alternately. They were mounted behind a perforated, rotating disc so as to provide two different flicker rates (5 fps and 15 fps) when the current (7.0 V) was switched from one bulb to the other. The speed of rotation was 1 rps. On average 50% of the light was let through. Each beam of light was projected onto and illuminated almost exactly the same area of the white reflecting board. The illumination, measured in the same way as in Experiment 1, varied between 3.5 and 4.8 Lux from one part of the training area to the other.

Of the four experimental groups two were constantly exposed to flashing light. The flashrates were 5 fps and 15 fps respectively for these two groups. For the other two groups the photic stimulation consisted of alternations between the two rates. Alternations were made according to the following schedule: During the first 63 sec rate A was administered for a period of 54 sec followed by a period of 6 sec for rate B and then by 3 sec of complete darkness. In continuation the time allotments for these successively administered conditions consisted of 21 sec for rate A (base rate), 6 sec for rate B (alternate rate), 3 sec of complete darkness. For one group the base rate was 5 fps and the alternate rate 15 fps, and vice versa for the other group. In the following description the blink frequency of the alternate rate is written as a subscript of the blink frequency of the base rate (rate A_{rate B}).

The chicks were assigned to the treatment conditions in blocks of four. Thus each of the four chicks in a block participated in one of the four conditions. Within blocks there was random assignment. Recall that in this experiment the black box served as imprinting object for all subject.

In addition to the three testing sessions described in Experiment 1,

a measure was also obtained in Experiment 2 of the imprinting object's attractiveness shortly after training. Thus, when the 12 min of training was completed the chick was transferred to a dark box where it remained while the floor of the alley was cleaned and the inserted wall removed. Five minutes after the end of training, the chick was placed in the middle of the alley with its head pointing towards a long side of the alley. The imprinting object was left in the same position as during training, i.e. midway along one of the short sides of the alley. The same source of light was used as before, but the flicker-producing device was never turned on in a testing session. Checks were made at 30 sec intervals during the first 6 min to determine the position of the chick in relation to the black box. If the chick had its whole body within the area 27 x 25 cm closest to the black box, a score of +1 was given. The corresponding area at the opposite end of the alley gave a score of -1, whereas a position in the intermediate area was scored 0. The attraction score of the object was the sum of all 12 observations during the 6 min testing session.

Results

The means of the attraction scores for the four experimental groups are presented in Table 2. The groups have been ordered according to

Table 2. Means of the attraction scores in Experiment 2 (n = 24).

Training condition	Single box after 5 min	Single box after 1 day	Single disc	Choice test
5	+1.58	+1.33	+ .38	-1.13
5 ₁₅	+ .92	+ .17	+ .75	- .17
15 ₅	-1.33	+ .13	+ .42	+ .21
15	-1.58	+ .33	+ .71	- .38

the proportion of low rate flashes contained in the stimulation. A nonparametric trend analysis (Ferguson, 1966) revealed a significant, monotonic, positive trend ($z = 2.06$, $p < .05$, two-tailed) in the

scores obtained shortly after training. As could be expected on the basis of different approach-eliciting properties of the two flash rates, a lower rate of stimulation during training resulted in a higher attraction score. None of the attraction scores for the groups on Day 2 exhibited a trend or an over-all difference that was significant. However, it is worth noting that for all groups the attractiveness of the single box on Day 2 was high in comparison to the results of Experiment 1. This was especially true for Group 5 (chicks constantly exposed to 5 fps).

Spearman rank correlations were calculated between start latency and the attraction scores for each of the experimental groups. Of the 16 coefficients obtained, only one was significant. Chicks in Group 5 with shorter latencies during training had higher attraction scores to the single imprinting object on Day 2 ($r_s = -.47$, $p < .05$, two-tailed). In contrast, chicks with negative attraction scores shortly after training, had significantly shorter latencies than chicks with positive attraction scores ($U = 8.5$, $n_1 = 11$, $n_2 = 6$, $p < .02$, two-tailed). A closer examination of the results revealed an interesting trend in the simultaneous choice test. As can be seen in Figure 1 there is a tendency for chicks preferring the imprinting object to exhibit extreme (short or long) start latencies when the proportion of low flash rate stimulation is high. This tendency is reversed in Group 15 (chicks constantly exposed to 15 fps). To analyse this trend statistically, the subjects in each group were first arranged in a series of increasing start latency. Then, a score of 1 was assigned to the chick with the shortest latency and also to the chick with the longest latency. A score of 2 was assigned to the chicks with the next shortest and next longest latencies and so on. Tied observations were assigned the average of the scores they would receive if no ties had occurred. A monotonic trend test for independent samples was then performed on the scores of the chicks preferring the imprinting object. The trend turned out to be significant ($z = 2.29$, $p < .05$, two-tailed). This means that as the proportion of higher rate stimulation is increased the resulting preference behaviour approaches that obtained in the constant light condition of Experiment 1, where chicks preferring the imprinting object were shown to have intermediate start latencies.

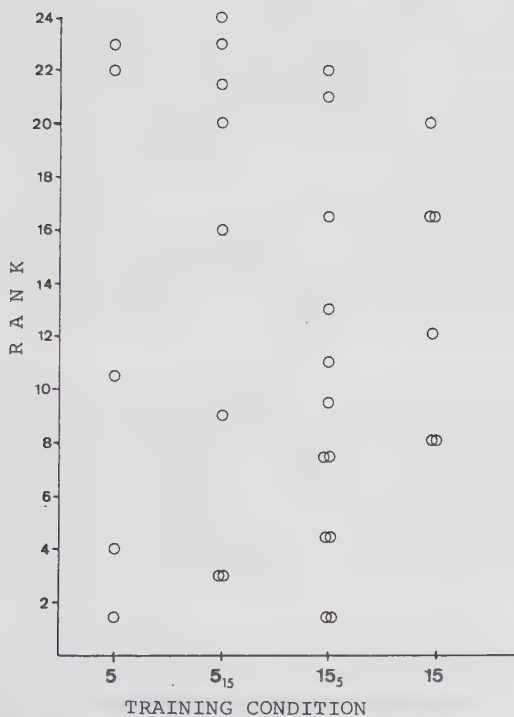


Figure 1. The relative start latency of chicks preferring the imprinting object in the simultaneous choice test. Chicks in each exposure group have been ranked separately. Rank 1 represents the shortest start latency.

The same trend was not evident in the total activity scores. However, for two of the four groups, the relationship to the scores obtained in the choice test was significant. The nature of the relationship differed between these two groups. For Group 5₁₅ the relationship was linear and negative ($r_s = -.52$, $p < .01$, two-tailed), whereas for Group 5 it was U-shaped; i.e. chicks preferring the imprinting object had more extreme activity scores than chicks preferring the novel object (Nonparametric test of relative variation in two independent samples $U = 7.5$, $n_1 = 13$, $n_2 = 5$, $p < .02$, two-tailed). Finally, in the latter group there was a positive correlation of marginal significance between total activity and attraction to the single imprinting object on Day 2 ($r_s = .35$, $p < .10$, two-tailed), which is in accordance with the negative correlation obtained for start latency.

Again the results in the high rate stimulus condition resemble those obtained in Experiment 1, where no systematic relationships were found with the total activity scores.

Discussion

The experiments presented here, reveal the existence of systematic relationships between indices of the chick's activity during training and the preference behaviour of the chick in a simultaneous choice test, i.e. when the chick is given a choice between the imprinting object and another, unfamiliar object. This is the most widely used procedure to decide whether a chick has become imprinted or not.

In Experiment 1, the chicks were exposed to either a black disc or a black box during training. The group exposed to the box, approached this object more in the simultaneous choice test than the group exposed to the disc. Thus, the short period of training did affect the preferences. However, as predicted, the disc was clearly superior to the box in inducing approach behaviour during testing. Such a strong influence of object characteristics on the results obtained in imprinting studies is not limited to studies using stationary objects but is also found when the birds are trained with moving models (see Klopfer, 1967).

In both training groups, start latency but not total activity was found to be significantly related to the preference behaviour in the simultaneous choice test. However, the nature of this relationship was not the same in the two groups. In the group trained with the intrinsically more attractive object, chicks which left the starting zone more quickly during training, subsequently showed a stronger preference for the imprinting object. This result seems reasonable from at least two points of view. Since there was a clear preference in this group for the imprinting object (only one chick preferred the novel object) the higher attraction scores of short latency chicks may not mean that they are more strongly imprinted but may simply reflect a repeated tendency to start walking more quickly. Moreover, a long start latency in a novel environment has often been interpreted as a fear reaction (Murphy, 1978), and it is possible that fear during training had a negative influence on the later preference for the imprinting object. The latter would also apply to the group trained with the box, but the low attraction scores shown by the chicks with the shortest start latencies in this group still require an explanation.

In Experiment 2, all chicks were exposed to the box during training, but the photic stimulation received differed between groups. Even in this experiment, start latency was found to be systematically related to the later preference behaviour in the choice test. The results for the group constantly exposed to the higher rate flashes were similar to those obtained for the box group in Experiment 1, i.e. chicks preferring the imprinting object had medium latencies. However, there was a trend toward a reversal of this pattern when lower rate flashes were increasingly included in the stimulation. Thus, there is an indication here that stimulus quantity is an important factor in changing the nature of the relationship. However, it should be pointed out that light flashing at a rate of 4 ± 2 fps has been found to have an extraordinary capacity to elicit approach responses in young chicks, and, hence, might not be a good representative of other low quantity stimuli. The two groups exposed to a majority of lower rate flashes were also the only groups in the present study in which a significant relationship emerged between the total activity scores and the later preference behaviour in the

choice test. It is possible that when such a relationship is found, the chicks have been exposed to a stimulus that is not easily adapted to and which accordingly continues to have a strong impact on the organism during the whole training session. This interpretation is consistent with the finding in many studies of sustained approach reactions to lower rate flashes (cf. above).

In a series of experiments, Bateson et al. have studied imprinting in day-old chicks to a rotating flashing light. In a typical experimental arrangement chicks were trained in running wheels kept at a fixed distance from a flashing light; either a red or a yellow stimulus object flashing at a rate lower than 5 fps. Later the preference behaviour of the chicks were studied in a simultaneous choice test involving these two stimuli. Some of the findings in these studies have implications for the interpretation of our data and will be summarized below.

When chicks were trained for 72 min, Bateson and Jaeckel (1974) found a weak but significant, positive correlation between the strength of preference for the familiar object and the total amount of approach activity during training. A measure of start latency during training showed no correlation with the preference scores. This indicates that total activity might be a better predictor of later preference behaviour when chicks are trained with lower rate flashes, which is in accordance with the discussion above.

A U-shaped relationship, similar to that obtained for the group constantly exposed to 5 fps in the present study, was observed by Bateson (1973) when the chicks were given 45 min of training with a flashing light. He interpreted his findings in the light of the results he obtained in still another study, this time of imprinting as a function of the length of exposure during training (Bateson and Jaeckel, 1976). In this latter study, Bateson and Jaeckel noticed a clear preference for the imprinting stimulus only after a short or an extended period of training, while at an intermediate length of exposure, the preference for the familiar object was less marked. Assuming that more active chicks had attended more to the stimulus, Bateson drew a parallel between the low imprinting scores for chicks

of medium activity levels and the decrease in preference for the familiar object after a certain length of exposure. Thus, the preferences of chicks of different activity levels were supposed to reflect different phases of the imprinting process; the tentative functional value of the temporary preference for "slight novelty" being the opportunities it offers for an adaptive exploration of the imprinting object from different angles.

One prediction that can be made from this model is that a U-shaped relationship between activity and preference for the imprinting object will be found after a longer period of exposure than an inverted U-shaped relationship. Since the latency data in Experiment 2 described a trend toward a reversal from an inverted U to a U-shape when the proportion of lower rate flashes increased in the stimulation, they can be taken to support Bateson's model if we make the assumption that the lower rate flashes speed up the imprinting process. Although this is a reasonable assumption, it is not so clear that this is the best way to interpret our data. In the present study a U-shaped relationship was found already after a much shorter period of training than that used by Bateson. Besides, it is uncertain whether we can expect more active chicks to have attended more to the imprinting object, since the chicks' movements were not necessarily approach movements towards the imprinting object.

An alternative interpretation is suggested by the data obtained when the box served as imprinting object, namely, that the chick will prefer the imprinting object if an optimal balance existed during training between the internal state of the bird and characteristics of the stimulation, e.g. stimulus quantity.

We do not know at present whether intermittent light is an aspect of the stimulation underlying imprinting in natural conditions, which was the idea held by James (1959) when he started to explore chicks reactions toward a flickering light source. However, in the chicken maternal call and in the pleasure notes of chicks we find sound emitted at what we have here defined as lower rates, and chicks attraction toward intermittent sound (as well as light)

centers on rates of 4 ± 2 pulses per sec (Collias and Joos, 1953; Gottlieb and Simner, 1969). Therefore, an interesting follow-up of the present study would be to explore whether intermittent sound has effects on retention which are similar to those found here for intermittent light.

A c k n o w l e d g e m e n t s

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EFFECTS OF VARIATIONS IN TRAINING CONDITIONS ON THE NATURE
OF THE RELATIONSHIP BETWEEN GENERAL ACTIVITY DURING TRAINING
AND THE STRENGTH OF IMPRINTING

by

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A b s t r a c t. - Three experiments were performed to study the activity of chicks during exposure to a stationary imprinting object in relation to preference behaviour in a later test session. The experiments were part of a series of studies exploring the possibility that reinforcing processes resulting from a balance between quantitative stimulus input and the arousal state of the chick play a role in imprinting. To create quantitatively differing stimulus input the imprinting object was presented together with intermittent light of two different rates and intensities. The results were compared with the findings in a previous, related study (Bengtsson, 1981). They suggest that the nature of the relationship between general activity during training and later preference behaviour in a simultaneous choice test varies with the quantitative aspects of the stimulation. Training chicks on the second day of life instead of on the first day of life resulted in a reduction in the number of imprinted chicks when higher rate intermittent light was administered during training.

The role played by reinforcement in imprinting has been difficult to assess. Many authors have conceptualized the imprinting object as an unconditioned stimulus or a consummatory stimulus, thus implying the capacity of the stimulation to function as a reinforcer (e.g. Bateson, 1973, Hess, 1973, Sluckin, 1972, Hoffman & Ratner, 1973). Experimental evidence for this capacity has also been obtained (Bateson & Reese, 1968, Hoffman, Eiserer & Singer, 1972). However, the importance of these reinforcement effects for the imprinting process has often been considered to be relatively low. This has been due partly to the fact that other aspects of the phenomenon have been stressed, such as e.g. exposure learning or genetic influences, partly to difficulties encountered when trying to fit the imprinting situation into a conditioning paradigm. A more recent exception to this position would appear to be the reinforcement model of imprinting presented by Hoffman and Ratner (1973). Referring to differences in the behaviour of birds towards stationary as compared with a moving object (whether imprinting or imprinted), the authors argue for the existence and importance of an innate reinforcing agent adhering in the stimulus-

pattern of a moving object. The capacity to elicit filial behaviour and to provide reinforcement is then thought to be conditioned to initially neutral features of the stimulus complex. Factors such as intermittent sound, visual flicker or physical contact in an imprinting situation are considered to provide reinforcement which is basically similar to that which is provided under conditions of visually perceived movement.

The interpretation of imprinting which emanates from the developmental theory of Schneirla (Moltz, 1963; Schneirla, 1965) also focuses on reinforcing processes. Moltz and Schneirla postulated that the reinforcement arises out of an optimal balance between stimulus quantity and the sensitivity of the organism. It is thought that by approach and following behaviour the birds regulate the level of stimulus input so that it is kept at an optimal level.

Bengtsson (1981) exposed groups of chicks to quantitatively differing photic stimulation (intermittent light of two different flash rates) in the presence of a static imprinting object. The training conditions did not allow the chicks to regulate the input level through approach or withdrawal in relation to the source of light. Since it is plausible that not all the chicks in a group have equal sensitivity, we could predict, on the basis of Schneirla's theory, that to some extent different chicks should imprint on quantitatively different stimuli. The results indicated that when the photic stimulation consisted of lower rate flashes, imprinted chicks exhibited extreme (low or high) activity during training compared to chicks which preferred the novel object in a simultaneous choice test, whereas in groups exposed to higher rate flashes more chicks of intermediate activity were imprinted. If the general activity of the chick reflects its sensitivity, these findings provide support for Moltz and Schneirla's positions.

The aim of the present study was to extend this analysis to new quantitative variations in the photic stimulation during training, and also to explore the effects of training at a later age when the internal state of the chicks may be supposed to have changed in important ways.

Experiment 1.

In a previous study (Bengtsson, 1981), a group of chicks was initially exposed to the imprinting object for 12 min during which the illumination consisted of light flashing uninterruptedly at 5 fps. Chicks which approximately 24 hr later preferred the imprinting object in a discrimination test were found to have exhibited extreme (low or high) ambulatory activity during the training period, whereas chicks of intermediate activity showed a preference for a novel, unfamiliar object. The aim of Experiment 1 was to study the nature of the relationship between the general activity during training and the later preference behaviour when the intensity of the light stimulation was higher than in the previous study.

Method

Subjects. Thirty domestic chicks of a broiler strain (Ross) were tested. Five separate batches of eggs were obtained from a commercial hatchery two days before hatching started. They were transferred to a still-air incubator where they were kept at a temperature of approximately 37.5°C. The humidity level was 85 to 90%. Within 8 hrs after hatching the chicks were transferred to rearing boxes where they were housed in groups of 3 to 8 chicks, the exact number depending upon how many eggs had hatched since the incubator was last inspected. From the moment the eggs were obtained at the commercial hatchery to the end of the experiment, efforts were made to limit the visual experience of the chicks outside of the actual experimental situation. The incubator and the rearing boxes were located in a room with blacked-out windows, and during the transportation between the rearing box and the experimental apparatus, the chick's head was covered in the experimenter's palm. Localisation of the chicks in the incubator and in the rearing boxes was mainly made by touch.

Apparatus and procedure. The apparatus and procedure were basically the same as that used in a previous study (Bengtsson, 1981).

At an age of 10 to 24 hr after hatching chicks were individually exposed for a period of 12 min to a stationary box (7 x 4 x 12 cm), covered with black velvet. The exposure (training phase) took place in

an area (27 x 18 cm) temporarily formed by inserting a wall into a larger alley (60 cm long x 27 cm wide x 30 cm high). The training area was divided into 6 zones of equal sizes (9 x 9 cm) by means of small markings on the walls. The number of zones entered by the chick during each 30 sec interval of the training phase were recorded. Two measures of the chick's general activity were obtained: 1) Start latency was defined as the ordinal number of the 30 sec interval in which 100% of the chick's body was outside the starting zone for the first time. The chick's starting position was in a corner by the inserted wall, where the chick was placed facing the imprinting object which was located midway along the short side of the alley. 2) Total activity was the sum of all zones entered by the chick with its whole body during the training phase.

The floor of the alley was a large plate of frosted glass which rested on a stand 105 cm high. All the light received by the chicks during training as well as during the testing sessions to be described below, came through the glass floor. Light from a distant source was projected against a tilted board located below the frosted glass floor, and the beam of light was reflected upwards, illuminating the whole floor. This experimental arrangement was used in order to minimize the possibility of the chicks to vary the intensity of photic stimulation received through approach or withdrawal in relation to the light source. Light was provided by a slide projector (Pentacon Filius 4) placed in front of the tilted board at a distance of 2.5 m. A sheet of cardboard, fixed close to the slide, stopped all light which did not pass through a small aperture (2 x 2 cm), and the intensity of the light was lowered by means of a rheostat so that a value of $16.4^{+0.4}$ Lux was obtained on a photometer (Lunasix) held perpendicular and close to the floor of the training area. The corresponding value when chicks were exposed to 5 fps in the previous study (Bengtsson, 1981) was $4.2^{+0.6}$ Lux, so in the present experiment the chicks were trained under a higher luminance level.

During the training phase, a disc with a dentation in the circumference was rotated closely in front of the projector lens and made the light flash at a rate of 5 fps. The speed of rotation was

1 rps, and on average 50% of the light was let through. The light/dark cycle had a marked sinoid shape. In these respects the stimulation did not differ from that presented in the previous experiment (Bengtsson, 1981).

After the chick had been exposed to the flashing light in the presence of the imprinting object for 12 min, the light was turned off, and the chick was transferred to a small box where it remained in darkness until 5 min had elapsed since the end of training. At this moment the chick was reintroduced into the alley where the inserted wall now had been removed and the floor cleaned. The chick was placed in the middle of the alley, facing one of the long sides. The imprinting object remained in the same position as during training, i.e. midway along either of the short sides of the alley. Constant, non-flashing light was provided by the projector. At 30 sec intervals the position of the chick was determined. Scores were assigned in the following manner: +1 was given if the chick had its whole body within the area 27 x 25 cm closest to the imprinting object. The corresponding area at the opposite end of the alley gave a score of -1, whereas a position in the intermediate zone was scored 0.

After 6 min the light was turned off, and the chick was removed from the alley. The attraction score of the object was defined as the sum of the twelve scores obtained. In order to control for position effects half the chicks were trained in one end of the alley and the other half in the other end of the alley. After the training phase a numbered ring was fixed around the left leg of the chick before it was returned to a communal rearing box where it was kept in darkness for 24 ± 4 hr until the commencement of the testing sessions on Day 2.

The testing phase on Day 2 consisted of three sessions in close succession. In the first session one half of the chicks was presented with the imprinting object and the other half with a novel object. The novel object was a disc, 15 cm in diameter, covered with black velvet. The disc was fixed to an anglebar which could be pushed in under the side of the alley. In this way the disc was elevated 2.5 cm above the floor, and a 3.75 cm² metallic rectangle was visible below

the disc. In the second session the chick was exposed to the object not presented in the first session, and, finally, in the third session there was a simultaneous choice test between these two objects.

A testing area (41.5 x 27 cm) was formed in the middle part of the alley by inserting black walls. This area was divided into three zones (two lateral zones 16 x 27 cm and one intermediate zone 9.5 x 27 cm) by means of small markings on the side of the alley. The objects were placed midway along the short sides of the lateral zones which were closest to the slide projector. A balanced sequence determined which object and which lateral zone was to be used in the first session. The object that was presented in the second session was always placed in the same position as the first object and remained in this position even during the last session when both objects were presented simultaneously, one in each of the lateral zones. The starting position of the chick in each session was in the intermediate zone close to the wall opposite to the object(s). Constant light was provided by the projector. Each session lasted for 3 min after which the chick was gently picked up and remained covered in the experimenter's palm while rearrangements were made in the testing area. The duration of an inter-test interval was always less than 30 sec. After the chick had been placed in the starting position, checks were made at 30 sec intervals to determine the position of the chick. In the first two sessions +1 was assigned if the chick was completely within the lateral zone containing the object, whereas -1 was scored in the other lateral zone. Remaining positions gave a score of 0. In the simultaneous choice test +1 was assigned in the lateral zone containing the imprinting object and -1 in the zone where the novel object was located. The sum of the scores in a session was called an attraction score, which accordingly could range from +6 to -6.

Ambient temperature was maintained at 23 to 24°C during training and testing by a radiator with a fan, which also provided a homogenous background sound. In the rearing boxes the temperature was approximately 30°C.

Results and discussion

In the test starting 5 min after the end of training the number of chicks having positive and negative attraction scores respectively, was approximately the same ($m = -.10$). The chicks which withdrew from the imprinting object had in most cases exhibited a higher total activity during training ($r_s = -.42$, $p < .05$, two-tailed). In a previous study (Bengtsson, 1981) when chicks were exposed to 5 fps at a lower intensity, it was found that in the same test, chicks which withdrew from the imprinting object had shorter latencies in the training phase than chicks with positive attraction scores. Accordingly, when chicks are exposed to light flashing at a rate of 5 fps a high general activity during the exposure seems in some way to be associated with a tendency to withdraw from the training area shortly after training.

The mean score for attraction to the box on Day 2 was very close to that obtained for the disc (Box, $m = -.17$; Disc, $m = -.20$). In neither of the two test sessions when the objects were presented alone could a systematic relationship to the indices of general activity be detected.

In the simultaneous choice test 9 chicks preferred the imprinting object and 13 chicks preferred the novel object ($m = -.47$). The rank positions of these 22 chicks on the two indices of general activity are shown in Figure 1. There was a tendency for chicks preferring the imprinting object to have intermediate scores on total activity. A nonparametric test of relative variation in two independent samples was applied to the data and revealed an effect of marginal significance ($z = 1.67$, $p < .10$, two-tailed). Since this relationship is the reverse of that found when chicks were exposed to the same rate at a lower intensity (Bengtsson, 1981), the data indicate that stimulus intensity is an important factor in determining the nature of the relationship between training activity and the later preference behaviour toward the imprinting object.

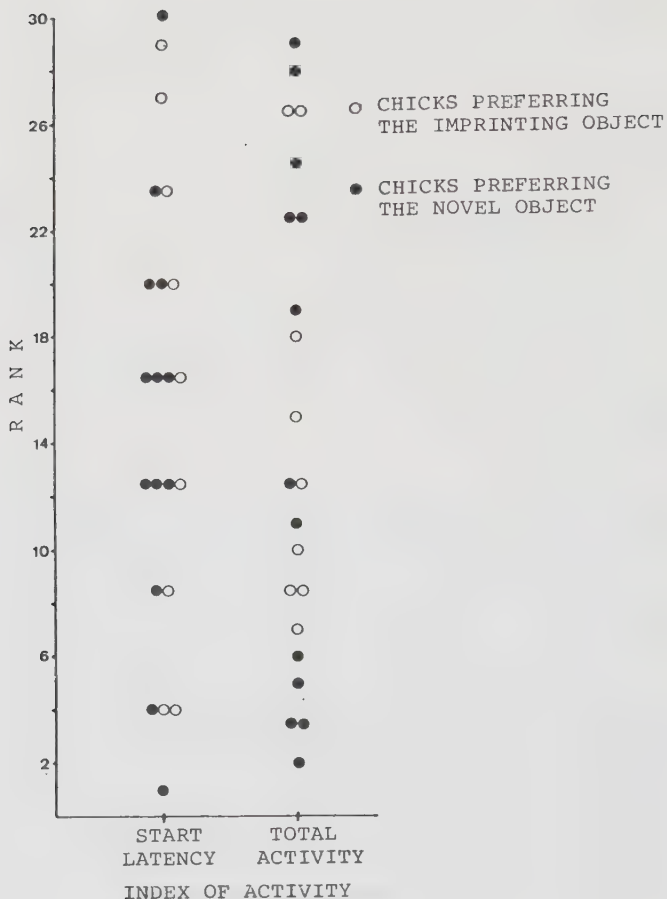


Figure 1. Relative start latency and total activity of chicks preferring the imprinting object and the novel object respectively. Rank 1 represents the shortest start latency and the highest total activity, respectively.

Experiment 2.

In Experiment 2, stimulus quantity was changed in relation to the previous study (Bengtsson, 1981) in such a way that the chicks were exposed to the photic training stimulation during a longer period. As before, the imprinting object was present for 12 min, but in this experiment exposure to the photic training stimulation started 12 min before the introduction of the imprinting object into the training field. Thus, the time offered to learn the characteristics of the training object was not changed.

Method

With a few exceptions to be described below, the apparatus and procedure were the same as in Experiment 1.

Twenty-six Ross chicks, hatched from three separate batches of eggs, were used as subjects. They were assigned to two experimental groups according to a balanced schedule. The experimental groups received the same treatment with the exception of differing photic training stimulation. The photic training stimulation was either constant light or light flashing at a rate of 5 fps. The intensity of the light was set at a level with that used by Bengtsson (1981). It was $4.4 \pm .4$ Lux in the training area when the flicker-producing device was off. The chicks were placed in the ordinary start position of the training area 10 to 24 hrs after hatching and were exposed to the photic training stimulation for 12 min with no imprinting object present (pretraining exposure). At the end of this period the chick was lifted up and remained covered in the experimenter's hand for 2-3 sec, while the imprinting object (the black box) was placed in the training area midway along the short side of the alley. In taking the chicks from the alley, the experimenter seized the chick gently, placing the palm of the hand over the head. Then the chick was put down again in the ordinary start position and given 12 min of exposure to the photic training stimulation in the presence of the imprinting object (training).

At the end of training the light was turned off, and the chick was picked up and returned to a rearing box after a numbered ring had

been put around its left leg. Measures of the chick's general activity were obtained both during training and during the pre-training exposure. In contrast to Experiment 1, no test was made of the imprinting object's attractiveness shortly after the end of training.

Results and discussion

Table 1 presents the means of the attraction scores obtained. The

Table 1. Means of the attraction scores in Experiment 2 ($n = 13$).

Training condition	Testing session		
	Single box	Single disc	Choice test
Constant light	+1.04	+ .13	+ .08
Flashing light (5 fps)	+ .38	+2.54	- .46

* Mann-Whitney test $z = 2.31$, $p < .05$, two-tailed

group exposed to flashing light (Group F) showed more approach towards the single disc than the group exposed to constant light (Group C). This unexpected difference is not easy to explain. However, it has been shown that the tendency to approach/follow a strange object can be enhanced by factors such as early handling or early aversive stimulation (Thompson and Dubanoski, 1964; Ratner, 1976), and perhaps the experimental stimulation for Group F had some nonspecific factor in common with those two types of stimulation.

Five different measures of the bird's general activity were analysed in relation to the approach behaviour. These five were: Start latency during pretraining exposure (a), total activity during pretraining exposure (b), start latency during training (c), total activity during training (d), and total activity during pretraining exposure plus training (e).

When the disc or the box was presented alone no systematic relation-

ships could be detected between the approach behaviour and any of these measures of activity. Results obtained in the simultaneous choice test are presented in Figures 2 and 3 for Group C and Group F respectively. Chicks exposed to constant light which later preferred

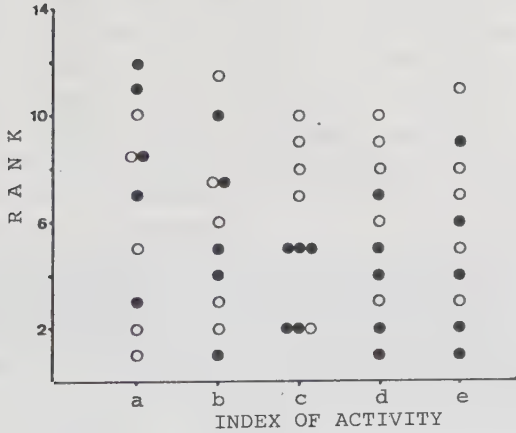


Figure 2. Rank positions of chicks preferring the imprinting object and chicks preferring the novel object on different indices of activity (a-e, cf. text). The chicks were exposed to constant light during training. Rank 1 represents the shortest start latency respective the highest total activity. Unfilled circles indicate chicks which preferred the imprinting object whereas filled circles stand for chicks which showed a preference for the novel object.

the imprinting object had longer start latencies and lower total activity during training than the chicks which preferred the novel object (in both cases Mann-Whitney $U = 4$, $n_1 = 5$, $n_2 = 5$, $p = .05$, two-tailed). Thus, in agreement with the findings in the previous study where chicks were trained under constant light without pre-training exposure (Bengtsson, 1981), start latency during training was systematically related to the later preference behaviour. The nature of the relationship was different, however; imprinted chicks having longer latencies instead of intermediate latencies in comparison to chicks preferring the novel object.

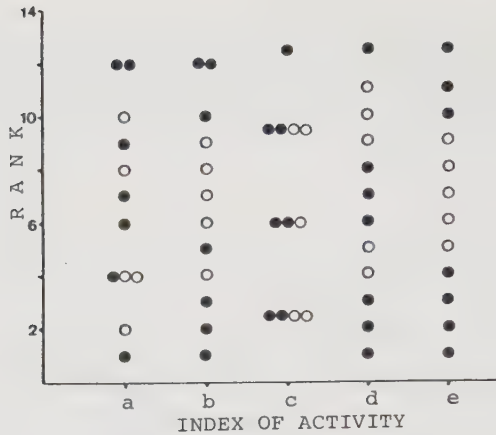


Figure 3. Rank positions of chicks preferring the imprinting object (unfilled circles) and of chicks preferring the novel object (filled circles) on different indices of activity (a-e, cf. text). The chicks were exposed to light flashing at a rate of 5 fps during training. Rank 1 represents the shortest start latency respective the highest total activity.

Imprinted chicks in Group F had intermediate scores on measures (b) ($U = 4.5$, $n_1 = 5$, $n_2 = 7$, $p < .05$, two-tailed) and (e) ($U = .5$, $p < .01$, two-tailed) compared to chicks preferring the novel object.

In the Bengtsson (1981) study, when the exposure to light uninterruptedly flashing at 5 fps ended after 12 min, it was found that chicks preferring the imprinting object had extreme total activity scores, whereas in the present experiment chicks with intermediate total activity scores during the first 12 min of exposure to the flashing light later preferred the imprinting object. Since, in the present experiment the imprinting object was not presented until after the end of the first 12 min period, this could mean that a quantitative level of stimulation, optimal in order for imprinting to take place, was reached after different lengths of exposure to flashing light for chicks with different reaction patterns. These conclusions must be regarded as tentative, since we cannot be sure that the results obtained in these two experiments can be meaningfully compared. In doing this, we have to make the assumption that

the approach/withdrawal test conducted shortly after training in the previous study did not critically affect the results obtained in the simultaneous choice test on Day 2.

The data from Experiments 1 and 2 in the present study suggest that a shorter period of exposure to flashes of a higher intensity may have had similar effects on the later approach and preference behaviour toward the imprinting object as a longer period of exposure to flashes of a lower intensity level. As we have seen, there was a tendency in Experiment 1 for imprinted chicks to exhibit intermediate total activity during training. In addition, when the scores obtained for attraction to the single imprinting object were correlated with the scores obtained in the simultaneous choice test, the surprising finding emerged that in Group F and in the group of Experiment 1, these two scores tended to be negatively correlated (Exp. 1: $r_s = -.44$, $p < .02$, two-tailed; Exp. 2, Group F: $r_s = -.55$, $p < .10$, two-tailed). An analysis of the same coefficients for all the groups in the previous study and for all other groups in the present study revealed that they were all close to zero, the largest values being positive.

Experiment 3.

The age of the chicks at the initial exposure to the imprinting object is one of the most important factors that determines the effects of the training. The tendency to exhibit fear reactions when first presented with a moving model increases during the first days after hatching (Hess, 1973). However, it has been demonstrated that when escape from the training situation is impossible, chicks and ducklings do develop a preference for the imprinting object even at a more advanced age, if the duration of the exposure is long enough (e.g. Ratner and Hoffman, 1974).

The older chicks that follow the model during training exhibit more intense following behaviour than younger chicks (Gottlieb, 1961; Bateson, 1964), and Kovach (1970) showed that the mean approach to optimal rate visual flicker increases in naive chicks reaching a peak at 3 days of age.

Accordingly, it has been well established that the way the young birds react to external stimulation changes over the first days after hatching, and the aim of Experiment 3 was to study the effects of training chicks at a later age under some of the photic training conditions used in the previous study (Bengtsson, 1981).

Method

Seventy-two Ross chicks were used as subjects. They were hatched in the laboratory and reared under similar conditions as the chicks in the previous experiments. For Experiment 3, eight batches of eggs were obtained from the commercial hatchery on separate days.

Part of the experimental equipment was changed in order to get the photic stimulation required for this experiment. The slide-projector was replaced by two small light bulbs with reflectors (6.3 V; .3A) which were mounted side by side 140 cm in front of the tilted board. The current could be switched from one bulb to the other from the experimenter's position. The lights were adjusted so that they illuminated almost exactly the same area on the tilted board. A disc could be rotated (1 rps) closely in front of the lights, and through perforations in the disc, two different flicker frequencies were obtained, one from each of the lights. The flash rates were 5 fps and 15 fps. As before, the disc let through 50% of the light on average, and the light/dark cycle had a marked sinoid shape.

Chicks were trained individually in blocks of three with random assignment within each block to three experimental conditions. One group was exposed for 12 min to light uninterruptedly flashing at a rate of 5 fps (Group 5). The photic stimulation for the second group (Group 5₁₅) consisted of repetitions of the following sequence: 5 fps during 21 sec followed by 15 fps during 6 sec and, finally, by 3 sec of darkness.

A different temporal stimulus pattern was administered only during the first 63 sec of the 12 min exposure period when the rate of 5 fps was given for an initial period of 54 sec followed by 6 sec of 15 fps and 3 sec of darkness. In the photic stimulation for the

third group the two rates changed places with each other, so that the higher rate was administered for most of the time. Accordingly, the proportion of lower rate and higher rate stimulation differed between groups.

In the previous study (Bengtsson, 1981), chicks were trained under these conditions during the first day after hatching, but in the present experiment ages ranged from 34 to 48 hr after hatching. Light intensity was the same in both experiments, i.e. 3.5 - 4.8 Lux measured in the training area at constant light, and, as before, an approach/withdrawal test to assess the attractiveness of the imprinting object was given 5 min after the end of training.

Results and discussion

The means of the attraction scores obtained in the various tests are presented in Table 2. Shortly after training, approach to the

Table 2. Means of the attraction scores in Experiment 3 (n = 24).

Training condition	Testing session			
	Single box after 5 min	Single box after 1 day	Single disc	Choice test
5	+ .58	+1.00	+ .83	- .75
5 ₁₅	+2.04	- .42	+ .92	-1.13
15 ₅	+1.92	-1.13	- .38	-2.29

imprinting object was about the same in all groups. However, in the test approximately 24 hr later, the groups differed significantly in their behaviour toward the imprinting object (Kruskal-Wallis $H = 6.21$, $p < .05$). Chicks constantly exposed to 5 fps had higher scores for attraction to the single imprinting object than chicks exposed to 15 fps during most of the training phase. Also in the simultaneous choice test chicks in Group 15₅ showed very low attraction to the imprinting object. Only one chick in this group preferred the box whereas 17 chicks preferred the disc. The over-all difference between groups was close to statistical significance ($\chi^2 = 4.89$, $p < .10$).

This is in clear contrast to the results obtained when chicks were trained at an earlier age (Bengtsson, 1981). Then, Group 15₅ contained the largest number of imprinted chicks (12 chicks preferred the imprinting object and 8 chicks the novel object). This change is accompanied by a drop in the mean approach to a source of light flashing at a higher rate (8.9 fps) between one and three days of age (Kovach, 1970).

Table 3. Spearman rank correlations between the indices of activity and the various attraction scores for different groups in Experiment 3.

Group	Index of activity	Testing session			
		Single box after 5 min	Single box after 1 day	Single disc	Choice test
5	Start lat.	-.53	-.45	-.35	+.32
	Tot. act.	+.14	+.23	+.26	-.54
5 ₁₅	Start lat.	-.15	+.16	-.28	+.48
	Tot. act.	+.14	-.25	+.01	-.44
15 ₅	Start lat.	-.17	-.06	+.03	+.28
	Tot. act.	+.18	-.22	+.19	-.13

Note $p = .05$, two-tailed for $r_s = .41$

Table 3 shows the Spearman rank correlation coefficients obtained between the two indices of general activity and the various attraction scores. It can be seen that in Group 5 approach to the single imprinting object was strongest among short latency chicks both shortly after training and in the test a day later. In both these tests there was a sufficient number of chicks with negative attraction scores to show that the correlation was not simply due to differences in the speed of approaching the object. Chicks with negative attraction scores had significantly longer start latencies during training than chicks with positive attraction scores (Shortly after training: Mann-Whitney $U = 4$, $n_1 = 7$, $n_2 = 4$, $p < .05$, two-tailed; One day after training: $U = 7$, $n_1 = 11$, $n_2 = 5$, $p = < .02$, two-tailed).

Similar results were obtained when chicks were trained on their first day of life (Bengtsson, 1981) but only in the test approximately 24 hr after training. In contrast, chicks which withdrew from the imprinting object shortly after training had shorter latencies than chicks which approached the object. This inconsistency suggests that some kind of transient over-stimulation can result from the exposure. Sluckin and Taylor (1964) used the concept of drive-satiation to explain findings which might be related to the present ones. Domestic chicks were exposed to a moving object for three hours. After this training session testing was begun either shortly after training or about half-an-hour later. Following of the imprinting object was found to be stronger after a longer time interval, suggesting a recovery from drive-satiation.

In the simultaneous choice test three significant correlations were found. In Group 5₁₅, chicks preferring the imprinting object tended to have exhibited longer start latencies and lower total activity during training. This means that the results are similar to those obtained when the training took place on the first day of life, except that no chicks with very short start latencies preferred the imprinting object when training took place at a later age (Fig. 4).

In Figure 5 the results for Group 5 are presented in the same way. In comparison to Group 5 chicks trained on the first day after hatching more chicks of intermediate activity level now preferred the imprinting object, whereas no chicks with higher total activity showed any sign of being imprinted. The start latency data retained a tendency toward a U-shaped relationship, with imprinted chicks found more at extreme values. A non-parametric test of relative variation in two independent samples was performed on the latency data from both age groups ($n = 48$). The latency scores of chicks preferring the imprinting object were tested against the latency scores of the chicks preferring the novel object. The scores were first ranked separately in each age group, and a statistical test was applied to these transformed scores. The difference in variation was statistically significant ($z = 2.08$, $p < .05$, two-tailed). Imprinted chicks had more extreme start latencies than chicks preferring the novel object.

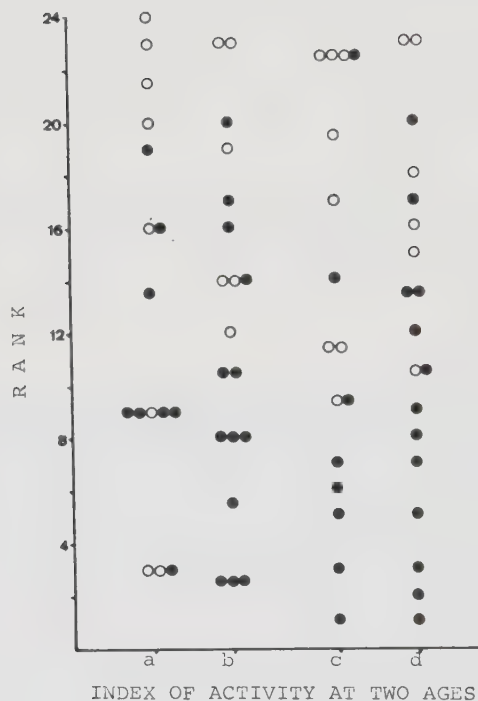


Figure 4. Relative start latency (a-b) and total activity (c-d) of chicks preferring the imprinting object (unfilled circles) and chicks preferring the novel object (filled circles) in the simultaneous choice test as a function of training age. Data are from Group 5₁₅ of Experiment 3 and from Group 5₁₅ of a previous study (Bengtsson, 1981). Rank 1 represents the shortest start latency respective the highest total activity.

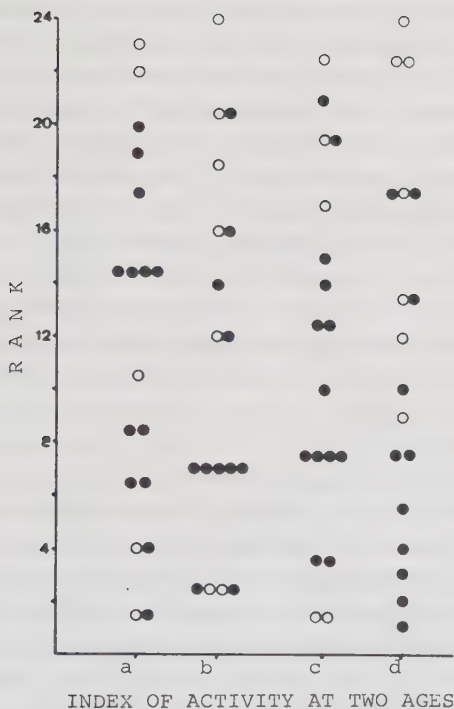


Figure 5. Relative start latency (a-b) and total activity (c-d) of chicks preferring the imprinting object (unfilled circles) and chicks preferring the novel object (filled circles) in the simultaneous choice test as a function of training age. Data are from Group 5 of Experiment 3 and from Group 5 of a previous study (Bengtsson, 1981). Rank 1 represents the shortest start latency respective the highest total activity.

We may conclude that in the simultaneous choice test the results obtained here did not differ much from the results obtained when chicks were trained at an earlier age under the same photic conditions. One important exception is the dramatic reduction in the number of imprinted chicks when the higher rate stimulation was given during most of the training period. This result offers some support to the idea that an optimal balance between the internal state of the chick and the quantitative aspects of the stimulation is necessary, if the chick is to prefer the imprinting object more than the novel object. With increasing reactivity in older birds we found a decrease in the number of chicks imprinted when exposed to the highest rate of stimulation, and in the group exposed only to lower rate flashes (Group 5) the results were very similar to those obtained in Group 5₁₅ when training took place at an earlier age.

G e n e r a l d i s c u s s i o n

Agents likely to produce general activation of the nervous system such as aversive stimulation, certain drugs, noise, and decreasing ambient temperature, have been shown to increase following and approach behaviour at the earliest ages (Pitz and Ross, 1961; Fischer, 1970; Hess, 1973). This facilitating effect can also be traced at re-exposure to the releasing stimulation. However, the intensity of excitation can be too high, even at the ages when the facilitating effect is most pronounced. This was noted by Kovach (1964) who found depressed following behaviour in chicks which were both injected with an autonomic drug and shocked during exposure to the imprinting object. The results of both the present study and the previous study (Bengtsson, 1981) are congruent with this pattern. Young chicks are known to be attracted to a source of light flashing at a rate of approximately 5 fps, and when the photic training stimulation consisted of light flashing at this rate for a short period and at a low intensity, chicks with shorter start latencies during training showed the strongest approach toward the imprinting object a day later. The same pattern was found shortly after training, when chicks were trained on the second day after hatching. Among chicks with positive attraction scores those with the shortest latencies during training were more attracted even

when chicks were trained at an earlier age ($r_s = .75$), $p < .01$), but, in this case, the chicks which had negative attraction scores had exhibited shorter latencies than chicks with positive attraction scores. Earlier we discussed the concept of drive-satiation in relation to this finding, but we can also seek an explanation in Kovach's demonstration that some kind of over-stimulation can counteract the tendency to approach (which of course is what we could expect on the basis of Schneirla's theory). This explanation would apply also to the finding of withdrawal reactions among chicks with high total activity scores in the group exposed to flashing light of a higher physical intensity.

Our data suggest that behaviour in the simultaneous choice test is regulated in quite a different way from behaviour toward the single imprinting object. Repeatedly we have found insignificant correlations between the degree of attraction to the imprinting object in the two different test sessions, and the only coefficient that reached significance was negative. A similar conclusion was reached by Fischer (1967) who studied imprinting in domestic chicks to a moving model which emitted calls. Chicks which were more active (reactive) during a short period just prior to training became strong followers but not necessarily better discriminators.

A finding by Barrett (1972), which was confirmed later by Ratner (1976), is also relevant in the present context. These investigators noted that aversive stimulation administered during training intensified the ducklings' following response, but, when offered a choice between the model used during training and a strange object, shocked chicks were more inclined to choose the strange object than were non-shocked controls.

On the other hand two studies which have related the activity of chicks during training to the preference behaviour in a later simultaneous choice test obtained results which suggest that the preference for the familiar object, just like approach to the single object, is strongest in chicks which are most active followers during training. Bateson and Jaeckel (1974) trained chicks for a total of 72 min with either a red or a yellow rotating light which emitted

flashing light at a low rate. Later the chicks were given a choice between these two stimulus objects. In both groups the initial choice was predominately in the direction of the familiar light, but the most vigorous approach response during the 5 min test was most often toward the red light. Giving the score a negative sign when the most vigorous approach response was in the direction of the novel object, the authors found a low, but significant, positive correlation between this measure of preference for the familiar stimulus and total approach during training. More strongly correlated, however, were the measures of start latency during training and testing as well as total activity during training and testing, and the differential strength of the most vigorous approach response could, hence, reflect persistent differences in activity. Following this line of reasoning, a positive correlation between preference for familiar and total approach during training may be expected on logical grounds, if a large enough majority of chicks showed the most vigorous approach to the familiar object.

Also the second study (Martin and Schutz, 1974) which reports a positive correlation between the diligence of following during training and later preference for the familiar object is open to some criticism. These investigators had mallard ducklings follow either of two models for 5, 10 or 20 min of total following. All nonfollowers were excluded from the experiment, which incidentally was a large proportion of the subjects. The ducklings' behaviour during training and in a later choice-test containing these two models indicated that one of the objects was intrinsically more attractive than the other object. In the group trained with the intrinsically more attractive object chicks which more quickly had attained the stipulated amount of total following during training, were found to show a stronger preference for the imprinting object. The index used for discriminative responding during the choice test was constructed so as not to be affected by the total amount of following by the bird, and, thus, the results are not open to the same criticism as was valid for the study by Bateson and Jaeckel discussed above. The positive relationship was not found in the group trained with the intrinsically less attractive object even though there was a tendency in the same direction among ducklings which had been

allowed to follow for 5 and 10 min. However, since the authors pointed out that no measurable learning occurred in these two subgroups, the conclusion that ducklings which followed more vigorously later showed a stronger retention effect should be restricted to the group trained with the intrinsically more attractive object, despite the fact that the positive relationship was significant for all groups combined. These results bear an interesting similarity to what Bengtsson (1981) found when domestic chicks were initially exposed to a stationary imprinting object under conditions of constant light. Chicks with shorter start latencies during training showed a stronger preference for the imprinting object but only in the group trained with the intrinsically more attractive object. Perhaps the initial attractiveness is most strengthened in more diligent birds, or, perhaps, the diligence reflects a stronger initial attraction to the imprinting object. We do not know for sure but another study by Martin (1975) may have implications for the choice of interpretation. In this experiment ducklings were injected with ACTH and after this they were exposed to an intrinsically attractive object which moved and emitted calls. Increased following was observed in this group in comparison to control ducklings which had received a saline solution, and also a stronger preference for the imprinting object in a later simultaneous choice test. This would seem to strengthen the view that learning was really more effective in more diligent chicks and ducklings.

However, our data suggest that we need something besides this to be able to explain how the object of lower initial attractiveness can gain control over the chick's preference behaviour, and the most reasonable explanation seems to be that for some chicks in each of our experimental groups, the imprinting object has come to signify a state of optimal balance between the internal state and the magnitude of external stimulation as a result of the exposure. This would bring a new dimension into the simultaneous choice test along which preferences could be demonstrated. Cheng et al. (1979) observed that ducklings which imprinted on a moving vocal model exhibited various signs of intermediate arousal during training. This finding seems reasonable and perhaps this is what we will always find when the birds are free to regulate their stimulative input level by

approach or withdrawal responses. However, the present results suggest that if this is the case, quantitative stimulus parameters will be operating to determine which birds will exhibit signs of intermediate arousal.

We may conclude that taken together, the findings in this paper and in the related previous paper (Bengtsson, 1981) are consistent with the views regarding the imprinting process presented by Moltz (1963) and Schneirla (1965). It should be pointed out, however, that the results, in at least one respect, have made the picture more complex. We have found that the development of an approach response to the single imprinting object is neither necessary nor sufficient in order for it to be preferred in a simultaneous choice test. This finding was obviously not anticipated by Schneirla who preferred to use the term approach-fixation instead of imprinting.

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